

Epiphytic relations of the Soft Tree Fern
Dicksonia antarctica Labill.
and the vascular plant species utilising its caudex

by

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Declarations

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of the candidate's knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Date

Abstract

This study fills a void in autecological research of *D. antarctica* by investigating the epiphytic relationships between the tree ferns and those vascular plant species which utilise its caudex. Research was based on hypotheses designed to explain aspects of the distribution of obligative epiphytes and the reliance of facultative epiphytes on *D. antarctica* caudices as well as why apogeotropic roots of terrestrially rooted specimens invade the tree fern's root mantle.

Close to 1200 specimens of Soft Tree Fern (*D. antarctica*) were examined in 19 replicate field plots representative of temperate moist forests in north-eastern Tasmania. *Dicksonia antarctica* morphological and site floristics variables were recorded from each site. Selected parametric and non-parametric statistical tests were employed to analyse the relationships between and among the observed and recorded environmental, morphological, floristic, epiphytic and apogeotropic variables.

Dicksonia antarctica frond plasticity was first examined because epiphytes are likely to be influenced both by site climatic conditions and by their host's architecture which in turn also influences microsite conditions. How frond size, frond frequency and frond shape change as *D. antarctica* grows older and taller was investigated using regression analysis. The inferred photosynthate store of *D. antarctica* was considered a critical determinant of emerging frond size and frequency. Frond size, frequency and shape were shown to vary with canopy closure, maximum temperature and site fertility. The relationships between caudex length and the size, frequency and shape of fronds are most likely indirect as a result of autocorrelation. The direct causal relationship is instead between the photosynthate store and frond size and frequency i.e. frond productivity.

Two main epiphyte zones were identified on *D. antarctica* caudices (stems). These zones were largely delineated by surface microclimate, texture and substrate conditions. The first zone consists of the lower caudex nearest the ground and is dominated by obligate hygrophytic vascular epiphytes. The second zone is at the apex of the caudex, which is colonised by obligate epiphytes that can survive a drier more exposed microclimate compared to the lower caudex. In between the lower caudex and caudex apex zones is typically a length of caudex which is largely devoid of obligate epiphytes.

Twenty-eight species of terrestrial flora were found to utilise large *D. antarctica* caudices as a regeneration substrate, providing strong evidence of the importance of *D. antarctica* caudices in maintaining floristic diversity in the closed-canopy wet forests of the region. *Dicksonia antarctica* caudices were identified as the dominant establishment substrate for *Atherosperma moschatum*, *Pittosporum bicolor* and *Tasmannia lanceolata* in these forests. *Nothofagus cunninghamii* can establish on all four substrates surveyed, provided there is sufficient insolation, but no single substrate dominates. *Olearia argophylla* seedlings were prolific across all substrates, but subsequent establishment success in general was poor and occurred only on soil and on erect *D. antarctica* caudices.

Atherosperma moschatum produces apogeotropic roots that invade the caudex of *D. antarctica*. Root invasion by *Atherosperma moschatum* may be instigated when *Atherosperma moschatum* roots in the soil detect a localised nutrient source of higher concentration in an adjacent *D. antarctica* caudex. A negative association was identified between apogeotropic *Atherosperma moschatum* root invasion and soil nutrient availability. It is possible *Atherosperma moschatum* is maximising access to nutrients on sites of low fertility compared to those on sites of high fertility. Apogeotropic root invasion was shown to be associated with a significant reduction in the frequency and size of fronds of the tree fern, compared to non-invaded caudices. Therefore apogeotropic root invasion constitutes a significant disadvantage to tree ferns as such an impost limits tree fern productivity and likely its ability to recover from periodic canopy disturbance and crown injury.

The contribution of *D. antarctica* caudices to forest biodiversity and in particular the population densities and regeneration modes of these important woody species suggest that excessive harvesting of *D. antarctica* caudices in concentrated areas, either legally or illegally, can be damaging to long-term forest diversity and structure. This study shows that the tree fern *D. antarctica* provides the principal regeneration substrate for several woody species in the moist closed forests of north-eastern Tasmania, including canopy tree species that are generally considered terrestrial (as opposed to epiphytic). The results demonstrate that *D. antarctica* exerts significant functional influence on forest structure and floristic composition of these forests, attesting to the essential role of the tree fern in contributing to the diversity and dynamics of these forests.

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List of Abbreviations and Terms

All sub.....	all substrates
ANOVA.....	analysis of variance general linear model
°C	degrees Celsius
C.....	canopy stratum
Canopy closure	sum of the mid-class foliage projective cover values of the high understorey, subcanopy understorey and canopy strata of a site.
Copp.....	coppice
CWD	coarse woody debris
DaC	erect <i>Dicksonia antarctica</i> caudex
Elev	elevated substrates (i.e. erect <i>D. antarctica</i> caudex, fallen <i>D. antarctica</i> caudex and coarse woody debris)
FAI.....	frond area index
FC	fallen <i>D. antarctica</i> caudex
FPC	foliage projective cover
GC.....	ground cover stratum
HUS	higher understorey stratum
Lamina width.....	lamina maximum width
Lower lamina length	lamina length from base to maximum width
Lower lamina percentage of length.....	lamina length from base to maximum width as a percentage of total lamina length
LUS.....	lower understorey stratum
Maximum temperature.....	the mean of daily maximum air temperature for the warmest month of the year.
Minimum temperature	the mean of daily minimum air temperature for the coldest month of the year.
MINITAB	a statistical program utilised to analyse data
na.....	not applicable
ns.....	not significant at $p > 0.05$
rainfall.....	mean annual rainfall
SC	subcanopy stratum
Upper lamina length.....	lamina length from tip to maximum width
Upper lamina percentage of length.....	lamina length from tip to maximum width as a percentage of total lamina length
VPD	atmospheric vapour pressure deficit

Chapter 1: Introduction

Dicksonia antarctica Labill. is a species of tree fern widespread throughout the understorey of south-eastern Australia's moist forests (Figure 1.1). The species is most abundant where there is a partially shaded environment, such as in small forest gaps, regeneration gaps and in the understorey of rainforest as well as along shaded forest edges and sheltered stream



Figure 1.1 An erect specimen of *D. antarctica* located on Mount Horror in north-eastern Tasmania.

banks (Figure 1.2). The erect rhizome of *D. antarctica* can grow up to 15 m tall (Large and Braggins 2004) although heights in the order of 7 - 8 metres are more common. The rhizome increases in height through the addition of fronds to a frond rosette present at its

apex (Figure 1.3). Croziers arise at the centre while old fronds are pushed out and to the underside of the rosette. The old fronds eventually die and detach, but the stipe bases of these fronds remain attached to the rhizome. The live fronds are positioned in such a way that they will funnel intercepted water and litter to the centre of the rosette. As croziers emerge litter becomes entangled around their stipes. With continual litter accumulation, and successive frond emergence, a debris ring can form. The debris ring erodes at its base, as old fronds detach, but some debris remains attached to the caudex around the stipe bases.



Figure 1.2 *Dicksonia antarctica* growing in a riparian situation near Lisle in north-eastern Tasmania.

From near the stipe bases fibrous roots grow down and around the rhizome (Large and Braggins 2004), forming the root mantle. In intermediate to mature plants the root mantle is present as a dense sheath up the majority of the rhizome, but progressively tapers toward its apex, leaving a layer of stipe bases and debris visible for the remainder of the caudex height of the fern. In the context of this study, the term caudex is used to define the erect rhizome of *D. antarctica* including its encompassing root mantle and protruding dead residual stipe bases.



Figure 1.3 A bird's eye view of the apical frond rosette of *D. antarctica* located on Mount Roland in northern Tasmania.

A mesic environment and a moist substrate favour epiphyte colonisation. Consequently the caudex of *D. antarctica*, with its high moisture retention properties (Roberts *et al.* 2005), is an ideal substrate for epiphytic (Mueck and Peacock 1992) and typically terrestrial flora (Ough and Ross 1992). The ease with which spores and seeds lodge in and roots penetrate the fibrous root mantle is also likely to increase the frequency and success of plant colonisation. Thus the establishment of flora, especially canopy dominants, on the *D. antarctica* caudex, complements its own presence and prominence in understorey vegetation (Figure 1.4). This suggests that the tree fern can exert a significant influence on forest structure and floristic composition (Ough and Ross 1992), potentially acting as an essential (possibly keystone) species in terms of its functional role in the diversity and dynamics of moist forest communities where it is prevalent. A keystone species is defined as a species whose effect is large, and disproportionately large relative to its abundance (Power *et al.* 1996).

The broad intent of this thesis is to analyse the relationships between *D. antarctica* and those vascular plant species which utilize its caudex as a substrate, either partially or completely, temporarily or in a lasting capacity. This will necessitate further understanding



Figure 1.4 A *D. antarctica* caudex (lower left) that has been colonised by multiple terrestrial plant species. Located on Mount Arthur north-eastern Tasmania.

of the host species in order to identify potential influences on those vascular species utilising its caudex. The thesis will address this by testing whether an allometric relationship exists between *D. antarctica* caudex length and its frond characteristics (size,

shape and frequency) and how these are influenced by the environment. The specific hypotheses to be tested in this area are:

- An allometric relationship exists where frond size, shape and frequency are dependent on caudex length.
- Frond size and frequency have a negative association with maximum temperature (the mean of daily maximum air temperature for the warmest month of the year) and minimum temperature (the mean of daily minimum air temperature for the coldest month of the year);
- Frond size and frequency are positively associated with inferred site fertility;
- Frond size and frequency are positively associated with rainfall (mean annual rainfall);
- Frond size and frequency are positively associated with canopy closure; and
- Variation in frond form is associated with maximum temperature (the mean of daily maximum air temperature for the warmest month of the year), minimum temperature (the mean of daily minimum air temperature for the coldest month of the year), rainfall (mean annual rainfall) and canopy closure variation.

Tree fern species have been shown to provide a regeneration substrate for typically terrestrial (i.e. facultative epiphyte) species in Jamaica (Newton and Healey 1989), New Zealand (Bellingham and Richardson 2006, Coomes *et al.* 2005, Gaxiola *et al.* 2008, Veblen and Stewart 1980) and Réunion Island (Derroire *et al.* 2007). Although facultative epiphytes have been observed growing in the caudex of *D. antarctica*, research into this subject in Australia is lacking. This thesis will address this deficiency by testing the following hypotheses:

- Established facultative epiphytes occur with greater frequency on *D. antarctica* caudices compared to other substrates such as soil and fallen logs or as coppice (for applicable species); and
- The height distribution of facultative epiphytes on *D. antarctica* caudices differs between seedlings and established plants of the same species. The reasoning behind this hypothesis is *D. antarctica* caudices may serve as a refuge from predatory or

environmental disturbances occurring on the forest floor that can lead to the death of seedlings nearer to the ground;

The microclimate at a particular location on the caudex will influence epiphyte success. Therefore those variables that influence microclimate at a particular location on the caudex, such as caudex aspect, height above the ground, caudex apical frond size, caudex apical frond frequency, caudex condition (i.e. surface texture and root mantle depth) and a site's broader climatic variables, such as minimum temperature, maximum temperature and rainfall (mean annual rainfall), can be expected to be associated with epiphyte establishment and frequency. Analysis of the effect of these variables on obligate epiphyte establishment and frequency will be achieved by testing the following hypotheses:

- Obligate and facultative epiphyte frequency and epiphyte species richness are positively associated with those parts of the caudex facing either a southern or eastern aspect as these provide a more mesic and sheltered microclimate;
- Obligate epiphytes occur at greater heights on those parts of the caudex facing either a southern or eastern aspect as these aspects provide a microclimate which is more sheltered from the wind and sun compared to the northern or western aspects. Accordingly mesic environments which favour the epiphytes extend higher on the caudex on the more sheltered aspects;
- Obligate and facultative epiphyte frequency will be greatest on the section of caudex that is thicker and therefore typically closer to the ground and hence more sheltered and with a greater moisture reservoir than other sections of caudex;
- Obligate epiphyte frequency and species richness on the tree fern caudex are positively associated with *D. antarctica* frond frequency and frond size. Larger more numerous fronds should provide an increasingly sheltered microclimate conducive to the epiphyte species of the lower *D. antarctica* caudex;
- Obligate epiphyte frequency and species richness are positively associated with canopy closure and rainfall (mean annual rainfall) as these two variables will augment the moist sheltered microclimate of the lower caudex;

- Obligate epiphyte frequency and species richness are negatively associated with maximum temperature (the mean of daily maximum air temperature for the warmest month of the year) as this variable should increase the desiccation risk to obligate epiphytes;
- Facultative epiphyte species frequency is negatively correlated with foliage projective cover (FPC) of the forest strata, *D. antarctica* live frond frequency and *D. antarctica* residual (marcescent) frond frequency. Shade cast by the overstorey and by the caudex fronds (alive or marcescent) can limit the light reaching facultative epiphytes, thereby affecting their germination and establishment success; and
- Facultative epiphyte species frequency is positively associated with the *D. antarctica* caudex length size class ≥ 3 m. Tree ferns this size are likely to be the oldest and possess a caudex with relatively thick rough textured root mantle in which facultative epiphytes can germinate and establish.

Roots that grow out of the soil and up tree stems are defined as apogeotropic. Ashton (2000) observed terrestrially sourced *Atherosperma moschatum* roots in the root mantle of *D. antarctica* in Victoria Australia. This leads to the questions of why *Atherosperma moschatum* roots do this and do they affect the host *D. antarctica*. Sanford's (1987) study of apogeotropic roots suggested a nutrient concentration gradient as a likely cause for their ascent. A similar cause could instigate the growth of apogeotropic *Atherosperma moschatum* roots into *D. antarctica* caudices. The presence of *Atherosperma moschatum* apogeotropic roots in the root mantle of *D. antarctica* is likely to place both species in competition for any nutrients present there and if *D. antarctica* is the loser this should be evident in the size and frequency of its fronds. This thesis will analyse these questions by testing the following hypotheses:

- The density of invaded *D. antarctica* caudices will be greater on sites of apparent low fertility compared to the density on sites of apparent high fertility;
- *Dicksonia antarctica* specimens invaded by apogeotropic roots have greater mortality and morbidity, than non-invaded *D. antarctica*;

- The density of invaded *D. antarctica* caudices will be greater on sites comprising topographic features that minimise soil depth compared to the density on sites comprising topographic features that maximise soil depth (relatively speaking);
- The density of invaded *D. antarctica* caudices will be positively correlated with rainfall and positively correlated with degrees of slope; and
- The density of invaded *D. antarctica* caudices will be positively correlated with the density of canopy/subcanopy stems.
- The density of *D. antarctica* caudices invaded by apogeotropic roots increases with the density of dominant (canopy and subcanopy) *Atherosperma moschatum* stems, and increases with the density of *D. antarctica* caudices.

The thesis comprises eight chapters including the Introduction. Subsequent chapters follow the sequence of Literature Review (Chapter 2), Site Selection and Field Sampling (Chapter 3), followed by Chapters 4 to 7 representing the core analysis and the interpretation of results. Chapter 8 presents a synthesis of the principal research outcomes.

The focus of the research is intentionally on vascular species. Although cryptogams constitute the majority of epiphytic diversity associated with *D. antarctica*, there have been detailed scientific investigations on this subject (Floyed and Gibson 2006, Roberts *et al.* 2003, Roberts *et al.* 2005). Consequently it was decided to focus on the lesser researched topic of vascular plant colonisation of *D. antarctica* and its implications for community structure and the dynamics of vascular plant populations. Keeping the research at a manageable size across an adequate array of sample sites in the time available was another important consideration in directing the research towards a particular focus on the analysis of caudex relationships with vascular plants.

The literature review (Chapter 2) concentrates on published research relevant to the utilisation of the *D. antarctica* caudex by vascular plants. Specifically, the review addresses topics such as the lower trunk epiphyte niche, the epiphyte colonisation of tree ferns, the

importance of tree fern caudices to the regeneration of typically terrestrial forest species and observations reported on the apogeotropic root phenomenon. An additional purpose of Chapter 2 is to identify gaps in present ecological knowledge of *D. antarctica*, gaps which this thesis will help to fill.

Chapter 3 (Site Selection and Field Sampling) details how and why the array of 19 sample plot sites were selected, as well as what variables were collected during field sampling and why. Chapter 3 does not include the particular treatment of analytical research methods as these are outlined in each of the subsequent experimental chapters in turn Chapters 4 – 7).

Chapter 4 addresses observations on *D. antarctica* frond plasticity and analyses the phenotypic variation of *D. antarctica* fronds in response to spatial and temporal variations in forest climate. *Dicksonia antarctica* frond plasticity was considered an important research topic in a thesis investigating the relationships between *D. antarctica* and its epiphytes. Epiphytes are likely to be influenced both by site climatic conditions and their host's architecture (viz. the nature and conditions of the frond and caudex).

Chapter 5 examines *D. antarctica* as a substrate for obligate epiphytes and analyses whether the epiphyte species identified during field sampling are associated with specific caudex characteristics (e.g. height, aspect and texture) and whether site conditions influence their frequency. This was considered an important focus of the thesis since the literature review identifies an absence of research into what parts or attributes of the variable *D. antarctica* caudex are preferred by obligate epiphyte species.

Chapter 6 analyses the regeneration of typically terrestrial plant species on *D. antarctica*, lists those species that were identified growing on the tree fern's caudex and examines the importance of the caudex to their regeneration under a mature wet forest canopy. The importance of tree fern caudices as a regeneration substrate for terrestrial species in New Zealand forests is highlighted by Bellingham and Richardson (2006), Gaxiola *et al.* (2008)

and Veblen and Stewart (1980). In south-eastern Australia, plant regeneration on tree fern caudices has only been observed qualitatively and not investigated quantitatively, consequently it is not known to what extent native species rely on the *D. antarctica* caudex for their regeneration relative to other substrates. Chapter 6 aims to remedy this.

The general phenomenon of apogeotropic roots has been described by Sanford (1987) in tropical Amazon forest and also by Reddell *et al.* (1996) in an Australian monsoon vine forest. Apogeotropic root invasion of the *D. antarctica* root mantle has only been briefly referred to by Ashton (2000). Therefore the common occurrence of the phenomenon across field sites in the current investigation provided an excellent opportunity to examine the relationship of *D. antarctica* and the invading woody species observed. Chapter 7 reports on observations of the invasion of the fibrous root mantle of *D. antarctica* by apogeotropic roots of *Atherosperma moschatum*. This work also examines the effect of *D. antarctica* becoming invaded with apogeotropic roots, specifically the effect on frond size and frequency. The attributes of site environment are also analysed to determine a possible environmental cause of apogeotropic root invasion.

The final chapter (Chapter 8) is a synthesis of the results of the four experimental chapters. This chapter brings together the principal research outcomes of the four preceding chapters and identifies important directions for future research.

By testing the hypotheses outlined above this thesis will evaluate evidence in support of the role of *D. antarctica* as a regeneration substrate for typically terrestrial species (i.e. facultative epiphytes). It will also show how the architecture of *D. antarctica* as well as a site's environment both influence the presence and distribution of facultative and obligate epiphytes on its caudex. The thesis will also show the extent to which *Atherosperma moschatum* can invade *D. antarctica* caudices via apogeotropic root growth and whether a site's environmental conditions are associated with the invasion.

Chapter 2: Literature review – *Dicksonia antarctica* tree ferns as a substrate for vascular plants

Introduction and overview

This chapter reviews the published literature applicable to the utilisation of *D. antarctica* by vascular plant species, namely the lower trunk epiphyte niche; the epiphyte colonisation of tree ferns; the importance of tree fern caudices to the regeneration of typically terrestrial forest species; and the apogeotropic root phenomenon. This chapter will conclude with an outline of the gaps evident in the present ecological knowledge of the epiphytic relations of *D. antarctica*.

Mention of *D. antarctica* in the scientific literature is more frequently due to its presence in the vegetation under study and therefore as a topic of contextual or background discussion or in a species index, rather than because it is the principal research subject (e.g. Ashton 1986, Ashton 2000, Garrett 1996a, Kirkpatrick *et al.* 1988, Mueck 1990, Mueck and Peacock 1992, Ough and Ross 1992, Wapstra *et al.* 2003). Pteridophyte reference books also include *D. antarctica* when relevant and typically provide a taxonomic description and a brief summary of the ecology and distribution of the species (Chaffey 1999, Duncan and Isaac 1994, Garrett 1996b, Large and Braggins 2004). Only limited detailed *D. antarctica* ecological research of *D. antarctica* has been published and typically has investigated either the species ecophysiology (Hunt *et al.* 2002, Volkova *et al.* 2010, Volkova *et al.* 2009a, Volkova *et al.* 2009b) or its relationship with epiphytic species (Floyed and Gibson 2006, Roberts *et al.* 2003, Roberts *et al.* 2005). Other research has investigated the survival of *D. antarctica* after clearfelling of forests (Ough and Murphy 2004), its regeneration (Chuter *et al.* 2008), its management and conservation (Unwin and Hunt 1995) and its life span (Mueck *et al.* 1996). Mueck *et al.* (1996) suggest *D. antarctica* has a life span of at least 500 years and because some individuals can survive catastrophic disturbances, such as fire and storm damage, they may be older than the surrounding canopy trees. A tree fern

management plan has also been published by the Tasmanian Forest Practices Authority, which outlines a system to facilitate and regulate the sustainable harvesting of *D. antarctica* in Tasmania (Forest Practices Authority 2007).

***Dicksonia antarctica* ecophysiology research**

The ecophysiological research of *D. antarctica* has revealed its extremely conservative water use strategy (Hunt *et al.* 2002) and its resistance to short-term severe water stress (Volkova *et al.* 2010). Hunt *et al.* (2002) showed that *D. antarctica* exhibits a strong stomatal response to atmospheric vapour pressure deficit (VPD). Increasing VPD results in stomatal closure, which limits gas exchange and therefore photosynthesis and photosynthate yield (Hunt *et al.* 2002). Hunt *et al.* (2002) proposed that the *D. antarctica* frond morphology may serve to funnel rainfall to the fern and maintain water relations. Both Hunt *et al.* (2002) and Volkova *et al.* (2010) came to the conclusion that the water use strategy of *D. antarctica* enables its success in an environment that can experience prolonged periods of non-optimal microclimate due to successional processes and pronounced seasonality (such as a wet sclerophyll forest understorey). *Dicksonia antarctica* has also been shown to experience chronic photoinhibition due to high irradiance, with temperature alone appearing to have no negative effect on photosynthesis (Volkova *et al.* 2009b). Volkova *et al.* (2009) suggested *D. antarctica* may be able to thrive under moderately high temperatures provided it is shaded.

Non-vascular epiphytes

Research of the relationship between *D. antarctica* and its epiphytic flora has focused primarily on bryophyte species (Floyed and Gibson 2006, Perpetua *et al.* 2005, Roberts *et al.* 2003, Roberts *et al.* 2005). A large diversity of bryophytes can colonise *D. antarctica* caudices with Roberts *et al.* (2005) identifying 81 species from sampling 120 caudices in southern and eastern Tasmania and Floyed and Gibson (2006) identifying 32 species from sampling 107 caudices in the central highlands of Victoria. Roberts *et al.* (2005) also sampled the bryophyte species colonising *Cyathea cunninghamii* Hook.f. and identified 52

species from 39 caudices, a comparable sample of *D. antarctica* caudices was calculated to support 64 bryophyte species. Both Roberts *et al.* (2005) and Floyed and Gibson (2006) came to the conclusion that *D. antarctica* provides a major substrate for bryophytes and is therefore an important component for maintaining forest diversity. However Perpetua *et al.* (2005) only identified seven bryophyte species that were positively associated with *D. antarctica* caudices compared to other potential substrates. This suggests *D. antarctica* can host a large diversity of bryophytes, but most of these also occur on other substrates. The presence of *D. antarctica* therefore increases the surface area available for bryophyte colonisation and each species frequency, but not necessarily bryophyte diversity as most species are also likely to have colonised other substrate types. On the other hand Perpetua *et al.* (2005) did not test the association of bryophyte species with *D. antarctica* as a combined substrate class, i.e. upright and fallen caudices. Some bryophyte species may be associated with *D. antarctica* caudices regardless of their orientation or may be associated with the reduced vertical surface of the fallen caudex.

The lower trunk epiphytic niche - tree ferns as a substrate

Vascular epiphytes of which there are estimated to be 29,000 species globally, occur in all forest strata with epiphyte diversity reaching 25 % of vascular flora in some tropical forests (Gentry and Dodson 1987). Tree ferns however occupy the lower forest strata and although considerable literature exists concerning epiphytes, this chapter only reviews literature pertinent to low trunk and tree fern epiphytes.

Kelly (1985) conducted an analysis of the vertical and horizontal distribution of all mechanically dependant life forms (including epiphytes) within a single area of Jamaican rainforest. He distinguished three broad epiphyte communities on large trees. One of these was a fern rich skiophytic community of the lower trunk, dominated by filmy ferns. In total, nineteen species of vascular epiphyte, including nine species of filmy fern, occurred in this lower trunk community. Similar fern rich epiphytic communities occupy the base of tree

trunks in forests elsewhere (Banaticla and Buot 2005, Dubuisson *et al.* 2003, Krömer *et al.* 2007, Mehltreter *et al.* 2005).

In addition to epiphytic colonisation of tree trunks, the caudices of large tree ferns are also colonised by epiphytes (Cortez 2001, Fraga *et al.* 2008, Mehltreter *et al.* 2005, Moran *et al.* 2003, Roberts *et al.* 2005). A tree fern caudex can be a superior epiphyte substrate compared to the basal trunk of neighbouring trees, due to their typically greater moisture and nutrient holding capabilities (Mehltreter *et al.* 2005, Moran *et al.* 2003) although this will vary among tree fern species (Roberts *et al.* 2005). A further characteristic of a tree fern's capacity for epiphytic colonisation of the caudex is their typically uneven surface comprising numerous pits and fissures (Derroire *et al.* 2007). These pits and fissures can enhance seed and spore lodgement on the caudex as well as help to maintain surface humidity, thereby preventing seed desiccation (Cortez 2001). The vertical surfaces of tree trunks do not typically possess such irregularities or unevenness of texture.

Tree ferns in Costa Rica for example were shown by Moran *et al.* (2003) to support a greater diversity of epiphytic ferns than nearby trees of comparable diameter at breast height. Eighty two species of epiphytic fern were identified as growing within three metres of the ground on either tree fern caudices or tree trunks, across four sites and on nine different tree fern species. Individually each of the four sites sampled by Moran *et al.* (2003) recorded an epiphytic fern diversity that ranged between nineteen and thirty three species and a filmy fern species richness that ranged between one and eight species. Moran *et al.* (2003) indicated that they did not sample trees with a diameter at breast height larger than that of the tree ferns and therefore the epiphytic fern diversity on the lower three metres of tree trunks could be higher than they identified.

Mehltreter *et al.* (2005) also compared the low trunk epiphyte diversity and frequency between angiosperm trees and tree ferns under the same macroclimatic conditions in a Mexican cloud forest. Fifty five epiphyte species were identified, including twenty two new

species, a large portion (twenty seven) being ferns (Mehltreter *et al.* 2005). Low trunk epiphytes represent a high percentage of the total epiphyte diversity in the cloud forest they sampled. However, only tree ferns of the smallest diameter at breast height range (5 – 10 cm) had greater epiphyte frequency and diversity per host than comparatively sized angiosperm trees. Mehltreter *et al.* (2005) attributed this to the tree fern's thicker root mantle and higher water retention capacity as well as being older in comparison to angiosperms of similar diameter at breast height. They also identified water content as the only bark/root mantle characteristic significantly correlated with epiphyte abundance, but not with epiphyte diversity.

Fraga, da Silva and Schmitt (2008) also investigated the composition and vertical distribution of epiphytic ferns on the tree fern *D. sellowiana* Hook., in an area of Araucaria forest in the state of Rio Grande do Sul of Brazil. They identified twenty species of vascular plant growing on *D. sellowiana*, all of them ferns, including twelve species of —habitual holoeiphytes”, i.e. obligate epiphytes. The lowest epiphyte abundance on *D. sellowiana* caudices occurred between three and four metres from the ground, which was thought due to the absence of the more frequent epiphytes at this height.

Cortez (2001) recorded the epiphytes found on thirteen species of tree fern in the cloud forests of Venezuela. Cortez (2001) recorded epiphytic fern species growing on *Alsophila erinacea* (H.Karst.) D.S.Conant, *Cyathea caracasana* (Klotzsch) Domin, *Cyathea divergens* Kunze, *Cyathea fulva* Fée, *Cyathea gibbosa* Bory, *Cyathea kalbreyeri* (Baker) Domin, *Cyathea microdonta* (Desv.) Domin, *Cyathea parianensis* (P.G.Windisch) Lellinger, *Cyathea pauciflora* (Kuhn) Lellinger, *Cyathea pungens* (Willdenow) Domin, *Cyathea senilis* (Klotzsch) Domin, *Cyathea squamata* Domin and *D. sellowiana*. However, across all of these tree fern species only fourteen epiphytic fern species, including eight filmy fern species, were recorded. Cortez (2001) did not report on the association of epiphytic species with their host species, but it was noted that fourteen fern species occurred predominantly on the basal adventitious roots comprising the root mantle of the

tree ferns, reportedly due to their apparent preference for the humidity and porous structure of this substrate.

The filmy fern dominance of lower trunk/caudex epiphyte communities is a common feature in many forests (Banaticla and Buot 2005, Cortez 2001, Kelly 1985, Krömer and Kessler 2006, Mehltreter *et al.* 2005, Moran *et al.* 2003, Parra *et al.* 2009). The success of epiphytic filmy ferns in the lower canopy can be ascribed to their hygrophilous epiphytic strategy (Dubuisson *et al.* 2003) and their shade tolerance (Proctor 2003), often matching with the increased water availability (humidity) and shade of the lower canopy (Dubuisson *et al.* 2003, Krömer *et al.* 2007). Zotz and Büche (2000) identified seven epiphytic filmy fern species occurring at a height less than five metres above the ground in a tropical lowland Panamanian forest. Whereas out of the eight species of filmy fern growing in Tasmania (Duncan and Isaac 1994), Roberts *et al.* (2005) identified five species growing on *D. antarctica* and four species on *Cyathea cunninghamii* all within three metres of the ground. Similarly Fraga, da Silva and Schmitt (2008) reported the decline in filmy fern frequency above a height of three metres on the caudex of *D. sellowiana* in the Araucarian forest in Brazil. Filmy ferns however are not restricted solely to the lower substrates as a few species have adapted to the more insolated and xeric conditions of the upper canopy (Krömer and Kessler 2006). Zotz and Büche (2000) for example identified a specimen of *Hymenophyllum brevifrons* Kunze at a height of 25 metres in the canopy.

Vascular epiphyte species also colonise the caudex of *D. antarctica* with 12 species of epiphytic fern using the tree fern as their principal host in Tasmania (Garrett 1996b). Little published research has been conducted into the relationship between *D. antarctica* and its vascular epiphytes with Roberts *et al.* (2005) being one exception. They showed that the diversity of epiphytic ferns at the caudex level was significantly higher on *D. antarctica* than on a co-occurring tree fern species *Cyathea cunninghamii*. The epiphytic ferns *Grammitis billardiarei* Willd., *Hymenophyllum australe* Willd. and *Hymenophyllum flabellatum* Labill. were positively associated with *D. antarctica* caudices. They also

measured the water holding capacity of the two tree fern species' root mantle and showed that on average the capacity of *D. antarctica* ($1168\% \pm 127\%$ of oven-dried weight) was significantly greater than that of *Cyathea cunninghamii* ($470\% \pm 56\%$). The greater substrate depth and water holding capacity of *D. antarctica* was considered an important factor promoting the diversity of its epiphytic fern flora. The reliance of endohydric ferns on their substrate for water and nutrients was considered a principal factor in this, making *D. antarctica* more amenable as a substrate alternative.

In comparison to ferns, bryophytes are predominantly ectohydric and are less reliant on their substrate to supply nutrients and water (Dubuisson *et al.* 2003, Roberts *et al.* 2005). Filmy fern species (of family Hymenophyllaceae) however are considered convergent with bryophytes due to their similar morphologies, i.e. very thin lamina and reduced vascular system (Dubuisson *et al.* 2003). This convergence may explain why only two filmy fern species out of the five identified by Roberts *et al.* (2005) were associated with *D. antarctica* caudices as they may not be as reliant on their substrate for moisture and nutrients, but more so on the amount and frequency of precipitation as well as high humidity. However, the low frequency of some filmy fern species on both *D. antarctica* and *Cyathea cunninghamii* across the field sites of Roberts *et al.* (2005) may also have resulted in the lack of statistical association. In comparison to *D. antarctica* as a substrate choice, a 1200 - 1300 year old Huon pine (*Lagarostrobos franklinii* (Hook.f.) Quinn) was identified by Jarman and Kantvilas (1995) to have supported thirteen vascular species as epiphytes, but only five of these were obligate epiphytes, three of which were filmy ferns.

Regeneration of terrestrial plant species on tree fern caudices

A large number of typically terrestrial plant species have been observed to be established on *D. antarctica* caudices, including the woody canopy dominants *Nothofagus cunninghamii* (Hook.) Oerst., *Acacia melanoxylon* R.Br., *Atherosperma moschatum* and *Phyllocladus aspleniifolius* (Labill.) Rich. ex Hook.f. (Ashton 2000, Ough 2001, Ough and Murphy 1996, Ough and Ross 1992, Roberts *et al.* 2005). Although not researched in

detail, the presence of established canopy dominants as well as other typically terrestrial plant species on *D. antarctica* caudices has lead Ough and Ross (1992) to suggest *D. antarctica* is important for the formation of the rainforest understorey.

Similar explanations have been identified with other tree fern species (Bellingham and Richardson 2006, Beveridge 1973, Coomes *et al.* 2005, Derroire *et al.* 2007, Gaxiola *et al.* 2008, Newton and Healey 1989, Veblen and Stewart 1980). For instance the caudex of *D. squarrosa* (Forst.) Sw. of New Zealand has been reported to facilitate the regeneration of several tree and shrub species by providing a substrate for regeneration and establishment (Bellingham and Richardson 2006, Coomes *et al.* 2005, Gaxiola *et al.* 2008, Veblen and Stewart 1980). Depending on prevailing conditions in the forest understorey, several species are restricted to elevated substrates, including tree fern caudices (Bellingham and Richardson 2006, Coomes *et al.* 2005, Gaxiola *et al.* 2008, Veblen and Stewart 1980). Conditions in the understorey that can restrict the establishment of seedlings to elevated substrates are shade (Coomes *et al.* 2005), litter accumulation (Bellingham and Richardson 2006, Coomes *et al.* 2005, Gaxiola *et al.* 2008), browsing (Gaxiola *et al.* 2008, Veblen and Stewart 1980) and seasonal riverine flooding (Unwin pers comm: west coast Tasmania, 20 June 2004).

Coomes *et al.* (2005), observed the near absence of seedlings on the ground under the multilayered canopy of fertile alluvial forest, but with the occurrence of many seedlings on elevated substrates, such as *D. squarrosa* and *Cyathea smithii* Hook.f. caudices. It was presumed by Coomes *et al.* (2005) that deep shade in addition prevented the establishment of seedlings on the forest floor and that tree fern caudices provided a substrate with better insolation above the dense ground cover. Examination by Coomes *et al.* (2005) of mature trees for signs of embedded tree-ferns in their trunks showed that 60% of *Weinmannia racemosa* L.f. had regenerated epiphytically. In contrast to fertile sites, the forest canopy on less fertile soil was more open and seedlings were plentiful on both the forest floor and elevated substrates. Nevertheless the small seeded *Metrosideros umbellata* Cav. and

Weinmannia racemosa still showed statistically significant preferences for elevated surfaces including on the caudex of *D. squarrosa* (Coomes *et al.* 2005). This study suggested these two small seeded species were susceptible to smothering by litter and are hence restricted to largely litter-free substrates, such as fallen logs and tree fern caudices.

Gaxiola *et al.* (2008) focused predominantly on how tree fern caudices facilitate seedling regeneration in productive lowland temperate forest. They argued that the general premise of small seeded species being shade intolerant is incorrect as their research demonstrated how small seeded species occurred epiphytically even though tree fern caudices are themselves shaded. A high proportion of individuals of the small seeded *Weinmannia racemosa* showed signs of epiphytic regeneration. Gaxiola *et al.* (2008) identified how the facilitative effect of tree fern caudices is species specific since shade tolerant species such as *Dacrydium cupressinum* Sol. ex Lamb. and *Prumnopitys ferruginea* (D.Don) de Laub. were not found on the forest floor, (presumably due to their inability to penetrate the dense ground cover) or on tree fern caudices. The seeds of *Dacrydium cupressinum* and *Prumnopitys ferruginea* were considered too large to successfully lodge in the surface of tree fern caudices.

Bellingham and Richardson (2006) also dealt with tree regeneration in temperate New Zealand rainforest, specifically the growth and survival of *Podocarpus hallii* Kirk, *Quintinia acutifolia* and *Weinmannia racemosa* seedlings over six years across three different microsites, i.e. soil, fallen logs and tree fern caudices. The study identified that *Quintinia acutifolia* and *Weinmannia racemosa* benefited from establishment on elevated substrates (logs and tree fern caudices), but not *Podocarpus hallii*, which was non-existent on tree fern caudices and did not differ in seedling frequency between soil and fallen logs.

Browsing also restricts the persistence of some species' seedlings on tree fern caudices (Gaxiola *et al.* 2008, Veblen and Stewart 1980). In New Zealand Veblen and Stewart (1980) investigated the effect of introduced herbivores by comparing the structure and

regeneration of forest on Stewart Island, which has a large introduced deer population, with that on Bench Island which has no deer population. On Stewart Island, large *D. squarrosa* caudices were found to be important requisites to the regeneration of several deer-preferred plant species, such as *Pseudopanax simplex* (G.Forst.) Philipson and *Myrsine australis* (A.Rich.) Allan, as they provided a seedling establishment site exceeding two metres height above ground, the approximate maximum browse height of deer. Unfortunately *D. squarrosa* themselves are also damaged by deer, such that their regeneration is inhibited, which in turn threatens the regeneration of other deer-preferred plant species (Veblen and Stewart 1980). Gaxiola *et al.* (2008) stated that deer are highly selective in their diet and accordingly have virtually eliminated seedlings of their preferred species from within the browse layer of many New Zealand forests. Their study identified the upper parts of standing tree ferns as the only places left for deer-preferred plant species to escape and to regenerate. It was proposed that large tree ferns provide refugia for the long-term persistence of highly palatable species. Although a large frequency of seedlings is generally found on fallen logs (Coomes *et al.* 2005), these would typically be lower than the maximum browse height of deer. It was unknown whether establishment of selected species on tree ferns was as important prior to the introduction of deer to New Zealand.

Beveridge (1973) proposed *D. squarrosa* as an important component in forest succession in providing a site for *Weinmannia racemosa* establishment, thereby indirectly facilitating podocarp regeneration. This occurs once mature *Weinmannia racemosa* develop an architecture suitable for perching birds which deposit podocarp (*Podocarpus* spp.) seeds at the base of the tree. By the time the *Weinmannia racemosa* is old and dying, a stand of podocarp saplings are present around the moribund tree, filling the resulting canopy gap (Beveridge 1973).

Weinmannia tinctoria Sm. on Réunion Island in the Mascarene Archipelago similarly has its regeneration facilitated by tree ferns. Three tree fern species, *Cyathea borbonica* Desv., *Cyathea glauca* Bory and *Cyathea excelsa* Sw. were identified by Derroire *et al.* (2007) as

aiding the persistence of *Weinmannia tinctoria*, a shade intolerant species, in late successional forest where canopy gaps for tree regeneration are rare. They considered tree ferns to facilitate *Weinmannia tinctoria* regeneration in two steps, the first is during seed dispersal by acting as a seed trap and the second during seedling establishment by providing a substrate with sufficient moisture and organic matter as well as greater access to light. Current distribution of *Weinmannia tinctoria* is considered dependant on the past distribution of tree ferns and the differential survival of seedlings.

Another species whose regeneration is facilitated by the tree fern *Cyathea pubescens* Kuhn, is *Clethra occidentalis* Kuntze. Newton and Healey (1989) reported that in Jamaican ridge-top montane rainforest 97 percent of *Clethra occidentalis* seedlings were growing in the adventitious root mantle of *Cyathea pubescens*. In addition, 51 percent of adult *Clethra occidentalis* showed signs that they began life epiphytically. Although *Clethra occidentalis* can regenerate within canopy gaps, these are rare in Jamaican ridge-top montane rainforests hence the establishment of *Clethra occidentalis* seedlings on *Cyathea pubescens* is considered vital for maintaining the relatively high density of this species in these communities (Newton and Healey 1989).

The apogeotropic root phenomenon

Epiphytes are not the only plants with access to the epiphytic substrate. The apogeotropic roots of some terrestrially rooted plant species are also able to grow up the trunk of trees or invade the caudex of tree ferns (Ashton 2000, Reddell *et al.* 1996, Sanford 1987). Sanford (1987) first researched the topic in nutrient poor Amazon *tierra firme* rainforest where apogeotropic roots were produced by 12 tree species across five families. He proposed that apogeotropic roots grew in response to a nutrient gradient in stemflow and tested his hypothesis by placing simulated stems, i.e. plastic pipes upright in the forest, topped with either cow manure, plant litter or nothing (the control). After eight months, the heights of apogeotropic roots on the artificial stems with manure averaged 18.2 cm, with litter averaged 3.6 cm and the control averaged 1.7 cm. The greater apogeotropic root

development on the manure pipes was taken to indicate that invading roots had shown a preference for the rich nutrient concentration of the manure which had been mobilised by rainfall. A similar explanation was considered for the litter and control pipes, but as these had smaller nutrient inputs and gradients they had correspondingly reduced root growth up the pipes (Sanford 1987). The nutrient gradient of the control pipes would have been naturally generated by rainfall or leached from vegetation in stemflow.

Reddell *et al.* (1996) also investigated the apogeotropic root phenomenon in Australian nutrient poor and seasonally inundated tropical rainforest. Eleven woody tree species representing eight families were observed to produce apogeotropic roots, which grew upwardly throughout the bark of 65% of tree stems with a diameter at breast height greater than 20 cm. The presence of apogeotropic roots on a tree stem was positively associated with flaky and papery textured bark. Similarly to Sanford (1987), Reddell *et al.* (1996) suggested that apogeotropic roots served the purpose of nutrient uptake in advance of stemflow reaching the soil, but also that they allowed root respiration and nutrient uptake during periods of inundation of the forest floor. The apogeotropic root phenomenon has not been researched in tree ferns. However Ashton (2000) did observe the presence of ground sourced *Atherosperma moschatum* roots in the root mantle of *D. antarctica* in south-eastern Australian wet eucalypt forest.

Conclusion

The review reveals a clear deficit in the published literature of quantitative research into the relationships between *D. antarctica* and those vascular plant species utilising its caudex. At To date only occasional field observations (Ashton 2000, Ough 2001, Ough and Murphy 1996, Ough and Ross 1992) and some biogeographic research into tree fern species in different environments (Bellingham and Richardson 2006, Beveridge 1973, Coomes *et al.* 2005, Derroire *et al.* 2007, Gaxiola *et al.* 2008, Newton and Healey 1989, Veblen and Stewart 1980) elude to the possible significance of the relationships. The need for such

research is critical to help reveal the importance of *D. antarctica* to forest regeneration, structure and floristic composition.

Harvesting of *D. antarctica* for the horticultural trade and its illegal poaching necessitate that this discrepancy is rectified in order to enable ecologically sustainable management of the forests it inhabits. This thesis fill the knowledge gap by investigating the relationships between *D. antarctica* and those vascular plant species which utilize its caudex as a substrate in north-eastern Tasmania.

Chapter 3: Site selection, field sampling, plot inventory and mensuration

Introduction

Dicksonia antarctica is a species of tree fern reaching its greatest fecundity in undisturbed moist forest, typically either rainforest or wet *Eucalyptus* forest (Forest Practices Authority 2007). Consequently 19 field sample sites representing replicates of the intact moist forest condition in north-eastern Tasmania were chosen for this investigation. Field sampling involved the recording of sample plot data necessary to reveal the relationships between *D. antarctica* and those vascular plant species which utilize its caudex as a substrate. These included the morphology, mensuration and parameterisation of *D. antarctica*, measuring and/or classifying those variables which define the broad environment condition of each sample site, the epiphytic associations with *D. antarctica*, evidence of apogeotropic root habit on *D. antarctica* caudices and associated floristic relationships.

Site description and location

Sample plots were located in north-eastern Tasmania. This area possesses a wide range of environmental conditions relating to altitude, topography, substrate, temperature, rainfall and vegetation, broadly representative of those in which *D. antarctica* can be found throughout Tasmania (Jackson 1999). A matrix of broad geographic and topographic conditions within the region was used to help select the sample sites across the range of different moist forest environments. Undisturbed field sites of mature moist forest were chosen within the matrix of environment categories according to the plan shown in Table 3.1. Within to the moist forest and riverine categories outlined, sample plot sites were selected to include at least 15 *D. antarctica* specimens, each with a well developed caudex per plot.

Table 3.1 The matrix used to categorise *D. antarctica* populations and site conditions present across north-east Tasmania. The matrix separates sites into two main elevation categories: $\geq 500\text{m}$ elevation and $< 500\text{m}$. Both of these categories are divided further by vegetation type and riparian situation.

	Highlands $> 500\text{m}$		Lowlands $< 500\text{m}$	
	Rainforest	Wet eucalypt forest	Rainforest	Wet eucalypt forest
Riverine	3	0	3	2
Non Riverine	6	2	1	2

Multiple 1:25,000 scale photo index type maps covering north-eastern Tasmania were purchased from Forestry Tasmania and used to identify areas of mature wet forest. Subsequent reconnaissance of these areas located field populations of *D. antarctica* within which a plot size of 20 m x 30 m (0.06 ha) would contain at least 15 live mature *D. antarctica*, surrounded by broad buffer areas of undisturbed forest. Each sample plot was surveyed along the contour and divided into 24 sub-plots of 5 m x 5 m. In all, 19 permanently marked replicates (sample plots) of the intact moist forest condition in north-eastern Tasmania were surveyed, containing 1135 individual specimens of *D. antarctica*, a sample considered sufficiently representative for statistical analysis (Table 3.2).

Field sampling

Site variables

Using an inclinometer (brand Suunto), Garmin GPS 72 and compass, the degrees of slope, slope aspect, and elevation (m) were recorded at each plot. Plots were placed into an aspect class and a topography class based on their proximity to permanent water (riverine/non-riverine) and degrees of aspect/slope (Table 3.3). Plot sites were further classified by fertility class based on the site's underlying geology (Silurian-Devonian sedimentary rocks (Mathinna beds) (Grant *et al.* 1995) = 1, and other geology, such as dolerite, or granite = 2). Fertility class 1 sites are of inferred low fertility, whereas fertility class 2 sites are of inferred high fertility. Riverine sites are sample plots situated within 10 m of permanent water.

Table 3.2 Details of the location, environment conditions and forest type of the 19 permanently marked sample sites surveyed. Max Temp is the mean of daily maximum temperature for the warmest month of the year. Min Temp is the mean of daily minimum temperature for the coldest month of the year. Rainfall is the mean annual rainfall. Temperature and rainfall were modelled by the software ANUCLIM 5.1 (McMahon *et al.* 2000).

Site Code	Forest Type	Riverine	Elev (m)	Long(E)	Lat(S)	Max Temp C°	Min Temp C°	Rainfall (mm)
01HLBRFR	Rainforest	Yes	290	147° 12' 45"	41° 18' 19"	21.90	1.80	1054
02HLBWSR	Wet Eucalyptus	Yes	270	147° 12' 35"	41° 18' 25"	22.00	1.90	1026
03MARRFR	Rainforest	Yes	646	147° 17' 52"	41° 15' 27"	19.30	0.80	1427
04MARRFR	Rainforest	Yes	660	147° 17' 42"	41° 15' 51"	19.30	0.80	1423
05MARRFR	Rainforest	Yes	651	147° 18' 15"	41° 15' 25"	19.30	0.80	1433
06MBWWSN	Wet Eucalyptus	No	716	147° 28' 06"	41° 23' 22"	19.00	0.40	1383
07CRKWSN	Wet Eucalyptus	No	460	147° 24' 45"	41° 17' 20"	20.70	1.40	1472
08SDLRFR	Rainforest	Yes	490	147° 24' 20"	41° 14' 20"	20.40	1.40	1488
09SDLRFR	Rainforest	Yes	500	147° 24' 20"	41° 14' 20"	20.30	1.40	1489
10SDLRFN	Rainforest	No	590	147° 24' 24"	41° 13' 37"	19.60	1.10	1494
11SDLWSN	Wet Eucalyptus	No	590	147° 24' 58"	41° 12' 59"	19.60	1.20	1501
12SDLRFN	Rainforest	No	585	147° 25' 09"	41° 12' 45"	19.60	1.20	1501
13MTMRFN	Rainforest	No	850	147° 42' 47"	41° 21' 14"	17.60	0.40	1374
14SPFRFN	Rainforest	No	725	147° 30' 08"	41° 17' 23"	18.70	0.60	1487
15SPFWSN	Wet Eucalyptus	No	480	147° 29' 35"	41° 17' 02"	20.50	1.40	1446
16MTHRFN	Rainforest	No	680	147° 43' 51"	41° 04' 09"	18.40	1.60	1581
17MTHRFR	Rainforest	Yes	460	147° 44' 46"	41° 04' 25"	19.80	2.30	1409
18MTHWSN	Wet Eucalyptus	No	230	147° 43' 00"	41° 05' 46"	21.30	3.00	1106
19LIFRFN	Rainforest	No	660	146° 45' 24"	41° 41' 21"	19.80	-0.40	1070

Table 3.3 Classes of site aspect and site topography. Topography classes are based on riverine location and degrees of slope.

Aspect	Aspect class	Riverine	Slope	Topography class
North-west	1	Yes	$> 5^\circ$	1
North	2	Yes	$\leq 5^\circ$	2
West	2	No	$\leq 5^\circ$	3
South-west	3	No	$> 5^\circ$	4
North-east	3			
South	4			
East	4			
South-east	5			

Rainfall (mean annual rainfall (mm/yr)), mean maximum monthly temperature ($^\circ\text{C}$) and mean minimum monthly temperature ($^\circ\text{C}$) for each plot were modelled by the software ANUCLIM 5.1 (McMahon *et al.* 2000), which uses plot coordinates and regional weather station readings to interpolate mean climatic variables for specified locations. In this study maximum temperature is defined as the mean of daily maximum temperature for the warmest month of the year, whereas the minimum temperature is the mean of daily minimum temperature for the coldest month of the year.

Sample plot sites were assigned to one of the classes (low/high) for each of the variables rainfall, maximum temperature and minimum temperature respectively (Table 3.4). The threshold values for each class were chosen to ensure both categories encompassed sufficient sites to enable statistical analysis. The assignment of rainfall, maximum temperature and minimum temperature values to classes instead of their use as continuous variables was necessary as these modelled variables did not possess a normal distribution and transformation was not successful.

Table 3.4 Classes assigned to maximum temperature (the mean of daily maximum air temperature for the warmest month of the year), minimum temperature (the mean of daily minimum air temperature for the coldest month of the year) and rainfall (mean annual rainfall) for each sample site.

Maximum temperature	Maximum temperature class	Minimum temperature	Minimum temperature class	Rainfall	Rainfall class
< 20 °C	Low (1)	< 1.3 °C	Low (1)	< 1400 mm	Low (1)
≥ 20 °C	High (2)	≥ 1.3 °C	High (2)	≥ 1400 mm	High (2)

For each sample plot, the percentage foliage projective cover (FPC) of the herb layer (< 0.20 m height above ground), ground cover (≥ 0.20 m to < 1 m height above ground), lower understorey (≥ 1 m to < 3 m height above ground), higher understorey (typically ≥ 3 m to < 10 m height above ground), subcanopy (typically ≥ 10 m to < 15 m height above ground) and canopy (typically ≥ 15 m height above ground) were visually estimated and placed into broad cover classes (Table 3.5) as outlined in Brower *et al.* (1990). The mid-class FPC value of each stratum was calculated for each plot (Table 3.5). Canopy closure was calculated for each plot by combining the mid-class estimates of FPC (including stratum overlap) for the higher understorey, subcanopy and canopy strata. Plots were placed into a class based on their percentage canopy cover (< 100 = 1 and ≥ 100 = 2).

Table 3.5 Cover classes based on percentage foliage projective cover (FPC) (Brower *et al.* 1990). The mid-class FPC value is used to calculate canopy cover of a site.

FPC	Cover class	Mid-class value (%FPC)
0 to ≤ 5 %	1	2.5
> 5 to ≤ 15 %	2	10
> 15 to ≤ 25 %	3	20
> 25 to ≤ 50 %	4	37.5
> 50 to ≤ 75 %	5	62.5
> 75 to ≤ 100 %	6	87.5

Site x species variables

The grid positions of each erect *D. antarctica* caudex and each tree present in the canopy and subcanopy were recorded. This was achieved by recording distance along the centre line of the plot and the perpendicular distance from the centre line to the specimen. Frequency of each vascular plant species and contribution to foliage projective cover (FPC) was recorded. Cover was visually estimated and placed into broad cover classes (Table 3.5)

as outlined in Brower *et al.* (1990) for each stratum for each of the following substrate types soil/litter, coarse woody debris (CWD), fallen *D. antarctica* caudices (FC) and erect *D. antarctica* caudices (DaC). Seedlings or suckers of woody species were classed as those present in the herb layer, i.e. < 0.20 m high. The diameter of all subcanopy and canopy stems were measured at 1.3 m above the ground (dbh). The crown spread along the four cardinal points and crown depth of all subcanopy and canopy stems were also recorded. The heights of each species present in the ground cover layer, lower understorey, higher understorey, subcanopy and canopy were recorded. To maximise the efficiency of sampling the herb layer, six 5 m x 5 m subplots out of the twenty-four subplots in each plot were selected at random to represent herbs. The six subplots were randomly selected from the 24 subplots by blindly selecting six numbers between 1 and 24 ‘out of a hat’. The aggregate frequency of each herb species respectively across the 6 subplots was divided by 6 and multiplied by 24 to represent each species frequency for the whole plot.

In addition to subcanopy and canopy species some understorey species such as *Olearia argophylla* (Labill.) Benth., *D. antarctica* and *Cyathea australis* (R.Br.) Domin, may be older than their overstorey (Mueck *et al.* 1996). Since there is a reported relationship between *Olearia argophylla* stem diameter (dbh) and stem age (Mueck *et al.* 1996), the dbh of large individuals of this species in the understorey were recorded.

Dicksonia antarctica variables

For each *D. antarctica* specimen, the following were recorded:

- erect caudex length (m),
- maximum caudex diameter (mm),
- frond length (mm),
- lamina maximum width (mm) (lamina width),
- lamina length (mm),
- the lamina length from tip to maximum width (mm) (upper lamina length),
- live frond frequency (frond frequency).

For each *D. antarctica* frond dimensional measurements were recorded from one healthy (no evidence of damage or disease) middle sized frond representing the upper frond layers of the rosette. For live *D. antarctica* caudices the erect caudex length was measured from the base of the caudex to where the stipe of live fronds emerges from the caudex apex.

For dead and still erect *D. antarctica* caudices, the erect caudex length was measured from the base of the caudex to the top of the remaining caudex. If a fallen trace was present representing the base of a caudex (dead or alive) the length of trace was recorded as was the direction in which it had fallen. The combination of erect caudex length and trace length is the fern's total caudex length. Four textural classes were defined to describe the surface texture of the caudex: Rough, Irregular, Frizzy and Debris Ring (Figure 3.1) the length of each of these on the caudex was recorded for each live caudex. The four texture types exist along the caudex length, always in the following order from base to apex: Rough, Irregular, Frizzy and Debris Ring, although some or any of the texture classes can be absent from a particular caudex. The rough surface texture consists of the lower and thicker sections of caudex where fibrous roots have enveloped residual stipe bases that are still attached to the rhizome. The irregular surface texture is the section of caudex where a relatively thin layer of fibrous roots has surrounded the residual stipe bases which still protrude from the caudex surface. Here the frizzy surface texture is the section of caudex where residual stipe hairs and other *D. antarctica* material cover the caudex to varying depths. The fibrous roots of the lower caudex textures are not readily visible and stipe bases protrude prominently from the caudex surface. The debris ring formation is not part of the caudex but is instead a loose covering of accumulated frond and litter debris that has become entangled around the stipe bases at the top of the caudex as new croziers emerge.

Each live *D. antarctica* caudex was allocated to a size class depending on total caudex length (Table 3.6). There were two size class types (A and B), which were used for different analyses (Table 3.6).



Figure 3.1 A mature specimen of *D. antarctica* on which the different caudex surface textures are evident. They are classed as rough (arrow), irregular (arrow) and frizzy (arrow). The base of the debris ring is also visible (arrow).

Table 3.6 *Dicksonia antarctica* size classes. Classes of Type A and B are based on the erect caudex length according to two different class groupings for respective analysis.

Caudex length	Size class (A)	Caudex length	Size class (B)
≤ 1.0 m	1	< 2.0 m	1
> 1.0 to ≤ 2.0 m	2	≥ 1.0 to < 3.0 m	2
> 2.0 to ≤ 3.0 m	3	≥ 3.0 m	3
> 3.00 to ≤ 4.0 m	4		
> 4.0 to ≤ 5.0 m	5		
> 5.00	6		

The crown width of *D. antarctica* specimens on the four cardinal directions, the maximum vertical projection of fronds above the caudex apex (not including newly emerged croziers)

and the degree of caudex tilt from the vertical and the direction of tilt were also recorded for each caudex. All *D. antarctica* caudices were placed in a health class of either dead = 0, or alive = 1.

Fron area index (FAI) was derived for each *D. antarctica* crown using the following procedure. Each frond was represented by a line drawing (Figure 3.2) based on lamina maximum width (a), lamina length (b), the length of frond between the frond tip and the maximum width (c), and the dimensions (d) and (e) which are defined as follows: $d = a/2$, and $e = b - c$. Dimensions c and d were used to estimate the area of the equal triangles **A**, and **B** where: Area = $(c \times d)/2$. Dimensions d and e were used to estimate the area of the triangles **C**, and **D** where: Area = $(e \times d)/2$. The frond area index (FAI) is defined in this study as the sum of the areas of the triangles **A**, **B**, **C**, and **D**. The crown area index (CAI) was calculated as the frond area index multiplied by frond frequency. Other frond variables were derived from the lamina length and width as outlined in Table 3.7.

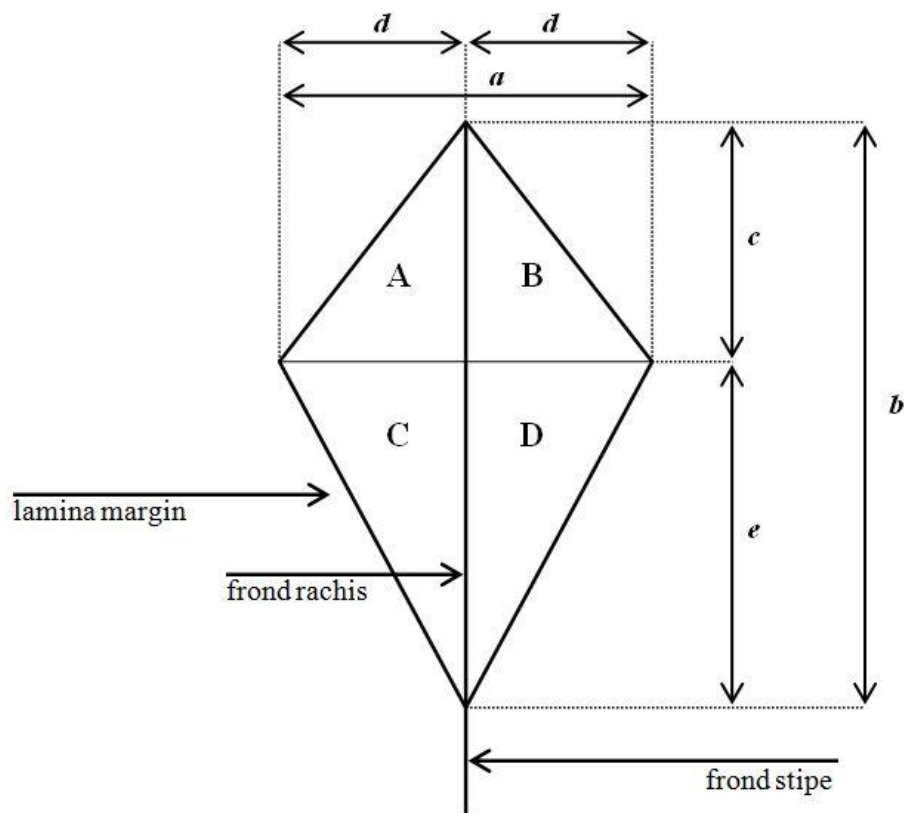


Figure 3.2 A *D. antarctica* frond represented schematically as a line drawing. Dimensions c and d were used to estimate the area of the equal triangles **A**, and **B** where: Area = $(c \times d)/2$. Dimensions d and e were used to estimate the area of the equal triangles **C**, and **D** where: Area = $(e \times d)/2$. The frond area index (FAI) is the sum of the areas of the triangles **A**, **B**, **C**, and **D**.

Table 3.7 Outline of additional frond variables derived from the lamina length and width dimensions. The first column lists the abbreviation used to identify the variable in the text and the analysis which follow in subsequent chapters of the thesis. The cross reference to Figure 3.2 column identifies where each variable sits in relation to a frond. Na, not applicable.

Abbreviated term	Description	Cross reference to Figure 3.2
lower lamina length	The length of the lamina from its base to its maximum width	<i>e</i>
upper lamina length	The length of the lamina from its tip to its maximum width	<i>c</i>
lower lamina percentage of length	The length of the lamina from its base to its maximum width as a percentage of total lamina length	na
upper lamina percentage of length	The length of the lamina from its tip to its maximum width as a percentage of total lamina length	na
ratio of upper and lower lamina length	the ratio of upper lamina length to lower lamina length	<i>e:c</i>
ratio of lamina width and length	the ratio of lamina width to lamina length	<i>a:b</i>

Epiphyte Variables

For obligate epiphyte species with a rosette growth habit (i.e. *Asplenium bulbiferum* G.Forst. and *Grammitis billardierei*) the distance from the base of the *D. antarctica* caudex and the aspect at which they occurred on the caudex (north, east, south or west) were recorded. The growth stage of *Asplenium bulbiferum* and *Grammitis billardierei* were also recorded as either sporeling or mature. Due to the spreading habit of rhizomatous species of obligate epiphyte, e.g. family Hymenophyllaceae, it was not possible to separate between individual plants. Instead the foliage projective cover (FPC) of rhizomatous species within a 29.6 cm x 21.1 cm area (called the sub-caudex sample plot) on the surface of each *D. antarctica* caudex was recorded at caudex heights above ground of 0.0 m, 0.2 m, 0.5 m and then every 0.5 m to the apex for each cardinal aspect (north, east, south or west). The 29.6 cm x 21.1 cm dimensions of a sub-caudex plot was chosen because it equals the area of an A4 sized transparency film which was used to outline each sub-caudex plot on the surface of the caudex. The transparency film enabled relatively easy estimation of the foliage projective cover (FPC) of each species in each sub-caudex plot. Typically terrestrial species of epiphyte found on *D. antarctica* caudices were treated the same as obligate rosette epiphytes, with the additional measurement of epiphyte stem length recorded.

To ensure adequate numbers for statistical analysis, only those epiphyte species identified to possess sufficient frequency and distribution across the field sites were included in this investigation. For obligate epiphytes, a frequency of 25 or more spread across the majority of sites was required. For woody terrestrial species occurring epiphytically, a frequency of 25 seedlings (< 0.20 m tall) or more occurring epiphytically across the majority of sites was required. The minimum frequency threshold values for the inclusion of species were determined after inspecting the data set of species' frequencies and distributions across the field sites. From these it was evident that species either occurred on a minimum of sites numbering < 25 specimens (for the whole range of plots) or occurred across the majority of sites and numbered in excess of 25 specimens (for the whole range of plots).

Apogeotropic Variables

Apogeotropic root invasion class was based on the degree to which apogeotropic roots were observed and visible around the exterior circumference of the tree fern caudex (no apogeotropic roots visible = class 0, a few apogeotropic roots visible around the exterior circumference of the root mantle (1 to \leq 4) = class 1, numerous apogeotropic roots visible around the exterior circumference of the root mantle ($>$ 4) = class 2). Each *D. antarctica* caudex was also assigned to another quantitative invasion class based on the visible presence or absence of apogeotropic roots around the exterior circumference of the caudex (no apogeotropic roots visible = class 0, apogeotropic roots visible = class 1). The maximum height above ground for which apogeotropic roots extended on a caudex, the maximum apogeotropic root thickness and the apogeotropic root thickness at the maximum height were also recorded. Species identification of *Atherosperma moschatum* apogeotropic roots was possible by the presence of the distinctive sassafras fragrance when roots were scratched. Other species' apogeotropic roots were identified through commonalities in texture and colour between the surface of the apogeotropic roots and the stems of surrounding tree species. The distance to the nearest potential source tree was also recorded for each invaded tree fern caudex.

Approach to analysis

Selected parametric and non-parametric statistical tests were employed to analyse the relationships between and among the observed and recorded environmental, morphological, floristic, epiphytic and apogeotropic variables. Regression analysis, Pearson's Correlation, Spearman's Rank Correlation, analysis of variance general linear model (ANOVA), Kruskal-Wallis test and Chi² analysis were employed where appropriate, using the statistical program MINITAB (2005), to investigate the relationships between and/or patterns within the variables associated with *D. antarctica* in the sample plots. Where the assumptions of parametric tests could not be met through transformation of data, a non-parametric equivalent was employed. The data analysed and the specifics of the statistical tests employed are outlined in each of the results and discussion chapters which follow (Chapters 4, 5, 6 and 7).

Chapter 4: *Dicksonia antarctica* frond plasticity in response to the forest environment

Introduction

Many plant species, both angiosperms and pteridophytes, show phenotypic plasticity in response to a heterogeneous environment (Callaway *et al.* 2003, Day 1998, Sultan 2000, Valladares *et al.* 2007, Weiner 2004). Leaf form for instance frequently changes with the prevailing light, moisture and temperature environment (Takenaka 1994), which enables photosynthetic gains to be maximised while minimising transpiration and photosynthate costs as well as optimising leaf temperature. The nutrient status of a plant can also influence leaf form with nutrient stress typically resulting in smaller and thinner leaves (Arens 1997). Based on this premise this chapter will test the hypothesis that:

- organ (frond) size and frequency are positively associated with increasing site fertility.

A plant's organ size also typically increases with plant size however this is not plasticity, but is instead an allometric relationship with larger plants able to allocate resources to the production of increasingly larger organs, e.g. leaves (Weiner 2004). In order to investigate whether an allometric relationship exists in *D. antarctica* this chapter will test the hypothesis that:

- *D. antarctica* frond morphological variables (e.g. size and shape) and frond frequency are dependent on caudex length.

The long life of *D. antarctica*, reaching at least 500 years (Mueck *et al.* 1996), can expose the tree fern to conditions that vary between a humid environment beneath a rainforest canopy, to an exposed environment following wildfire (Hunt *et al.* 2002). Even if macroclimatic seasonal variability is minimal, the apically situated *D. antarctica* fronds are exposed to an increasingly xeric microclimate as the tree fern increases in height (Dubuisson *et al.* 2003). Furthermore *D. antarctica* has a strong stomatal response (closure)

to increasing vapour pressure deficit (VPD), which limits carbon uptake and photosynthesis and infers low rates of water transport within the fronds under advective conditions (Hunt *et al.* 2002). Consequently morphological plasticity of emerging fronds in response to the prevailing conditions may enable *D. antarctica* to reduce water loss in a xeric microclimate while maximising photosynthesis. The strong stomatal response of *D. antarctica* with increasing VPD (Hunt *et al.* 2002) should limit CO₂ uptake, photosynthesis, the amount of photosynthates available for frond production and therefore also the size and frequency of fronds. Since increasing VPD is caused in part by increasing temperature and low water availability the current chapter will test the hypotheses that:

- Frond size and frequency have a negative association with maximum temperature (the mean of daily maximum air temperature for the warmest month of the year) and increasing minimum temperature (the mean of daily minimum air temperature for the coldest month of the year);
- Frond size and frequency have a positive association with increasing rainfall (mean annual rainfall); and
- Frond size and frequency have a positive association with increasing canopy closure (Increasing canopy closure should result in a more shaded microclimate in the understorey and lower VPD).

If *D. antarctica* exhibits phenotypic plasticity in response to a heterogeneous environment then such a response, e.g. changes in leaf form (Takenaka 1994), could be expected to be associated with changes in maximum temperature, minimum temperature, rainfall, and canopy closure. In this chapter leaf form is represented as the ratio of upper lamina length to lower lamina length, the ratio of lamina width and lamina length, upper lamina percentage of lamina length, and the lower lamina percentage of lamina length. Therefore the current chapter will test the hypothesis that:

- phenotypic plasticity is evident by the association of variation in these leaf form variables with variation in maximum temperature (the mean of daily maximum air temperature for the warmest month of the year), minimum temperature (the mean of

daily minimum air temperature for the coldest month of the year), rainfall (mean annual rainfall) and canopy closure.

Analysis

The environmental and morphological variables associated with *D. antarctica* were observed and recorded in the sample plots described in Chapter 3 (Site Selection and Field Sampling). The site environmental variables used in this chapter are canopy closure, maximum temperature (the mean of daily maximum air temperature for the warmest month of the year), minimum temperature (the mean of daily minimum air temperature for the coldest month of the year) and fertility class. These variables were assigned one of two classes with class 1 always comprising lower values than class 2. Refer to Table 3.4 for how the maximum temperature, minimum temperature and rainfall classes were delineated and Table 3.5 for how the canopy closure classes were delineated. The site fertility was assigned one of two classes based on the site's underlying geology (Grant *et al.* 1995). Class 1 sites consisted of inferred low fertility compared to class 2 sites which are of inferred high fertility. Refer to Chapter 3 for the details of how the site fertility classes were delineated.

The morphological variables associated with *D. antarctica* used in this chapter are erect caudex length, debris ring length, frond frequency, frond length, lamina length, lamina maximum width (lamina maximum width), upper lamina length (the length of the lamina from its tip to its maximum width), lower lamina length (the length of the lamina from its base to its maximum width), frond area index (Figure 3.2), crown area index, vertical frond projection (maximum vertical projection of the frond rosette above the top of the caudex), upper lamina percentage of length, lower lamina percentage of length, the ratio of upper to lower lamina length, and the ratio of lamina width and length. The details of the morphological variables associated with *D. antarctica* are outlined in Chapter 3, including Table 3.7.

The fitted line plot regression analysis ($\alpha \leq 0.05$) (MINITAB 2005) was used to test the hypothesis that *D. antarctica* frond morphological variables and frond frequency are dependent on erect caudex length. The regression fitted line plot produced by MINITAB was used to display the relationship between erect caudex length and each of the frond morphological variables.

Analysis of variance using the General Linear Model (ANOVA) ($\alpha 0.05$) (MINITAB 2005) was used to test the following hypotheses:

- organ (frond) size and frequency are positively associated with increasing site fertility.
- Frond size and frequency have a negative association with maximum temperature (the mean of daily maximum air temperature for the warmest month of the year) and increasing minimum temperature (the mean of daily minimum air temperature for the coldest month of the year);
- Frond size and frequency have a positive association with increasing rainfall (mean annual rainfall);
- Frond size and frequency have a positive association with increasing canopy closure; and
- phenotypic plasticity is evident by the association of variation in these leaf form variables with variation in maximum temperature (the mean of daily maximum air temperature for the warmest month of the year), minimum temperature (the mean of daily minimum air temperature for the coldest month of the year), rainfall (mean annual rainfall) and canopy closure.

The environmental class variables (canopy closure, fertility, rainfall, maximum temperature and minimum temperature) were included as factors together in an ANOVA model with lamina width included as the sole response variable. *Dicksonia antarctica* caudex erect length was selected as a covariate in order to remove background variability caused by differing fern ages and heights in the data set. Separate ANOVA were undertaken using each of the remaining frond variables (vertical canopy height, frond frequency, frond length, lamina length, upper lamina length, lower lamina length, upper lamina percentage

of length, lower lamina percentage of length, ratio of upper to lower lamina length, ratio of lamina width and length, CAI and FAI) as individual responses, while retaining the same factors and covariate. When ANOVA was conducted using vertical frond projection as the response, the variables frond frequency and frond length were selected as additional covariates as these could influence the distance fronds project above the caudex apex. For each of the individual ANOVA if a factor was identified by MINITAB as being non-significant then that factor was removed and the model recalculated. For each environmental variable identified to contain a significant variation among its classes the Tukey test, provided as part of the ANOVA option in MINITAB, was used to identify those classes between which the significant variation occurred.

Dicksonia antarctica specimens hosting large facultative epiphytes or apogeotropic roots or having recently fallen over were removed from the data set to reduce the influence of these variables on the results of regression and ANOVA analyses. Juvenile *D. antarctica* (i.e. a caudex length of 0 metres) were also removed from the dataset as these prevented the normal transformation of the *D. antarctica* caudex erect length and therefore regression and ANOVA analyses using this variable.

The *D. antarctica* frond morphological variables were transformed using the Johnson Transformation or Box Cox Transformation (optimal Lambda) in MINITAB in order to meet the normal distribution assumption of regression and ANOVA. The homogeneity of variance of *D. antarctica* frond morphological variables among environmental variables was confirmed using the 2 variances option in MINITAB.

Results

All frond morphological variables were each significantly dependant on erect caudex length, indicating the presence of a possible allometric relationship (Table 4.1). The relationships were best expressed as nonlinear equations, indicating that changes in each frond variable were not proportional to changes in *D. antarctica* erect caudex length, as

evidenced by the polynomial regression lines (Figure 4.1). Most frond morphological variables show a predominantly positive relationship with *D. antarctica* caudex erect length. The exceptions to this are upper lamina percentage of length, ratio of upper to lower lamina length, and ratio of lamina width and length which show a predominantly negative relationship with caudex erect length (Figure 4.1).

Table 4.1 Results of regression analyses ($\alpha \leq 0.05$) of *D. antarctica* erect caudex length versus *D. antarctica* frond morphological variables. (***, $p \leq 0.001$).

Dependant Variable	R ² Adj
Debris ring length	3.6 % ***
Frond frequency	38.2 % ***
Frond length	34.2 % ***
Lamina length	38.7 % ***
Lamina width	23.0 % ***
Upper lamina length	23.8 % ***
Lower lamina length	35.1 % ***
Frond area index	36.4 % ***
Vertical height of canopy	10.6 % ***
Upper lamina percentage of length	16.7 % ***
Lower lamina percentage of length	16.7 % ***
Ratio of upper to lower lamina length	16.9 % ***
Ratio of lamina width and length	28.0 % ***

The increase in upper stratum canopy closure from canopy closure class 1 (low) to class 2 (high) represents a decrease in sunshine reaching the understorey. Frond frequency, frond length, lamina length, upper lamina length, lower lamina length, upper lamina percentage of length, ratio of upper to lower lamina length, CAI and FAI all decrease from class 1 (low) to class 2 (high) canopy closure (Appendix 1, Table 1.1) and therefore also with decreasing sunlight exposure of *D. antarctica* in the understorey. However, lower lamina percentage of length increases from class 1 (low) to 2 (high) canopy closure as does the ratio of lamina width and length (Appendix 1, Table 1.1). The increase in lower lamina percentage of length also represents a decrease in upper lamina percentage of length meaning the lamina maximum width is closer to the lamina tip (Appendix 1, Table 1.1). Lamina width does not vary between canopy closure classes. The decrease in lamina length with increasing canopy closure, (without change in lamina width) is also revealed by the

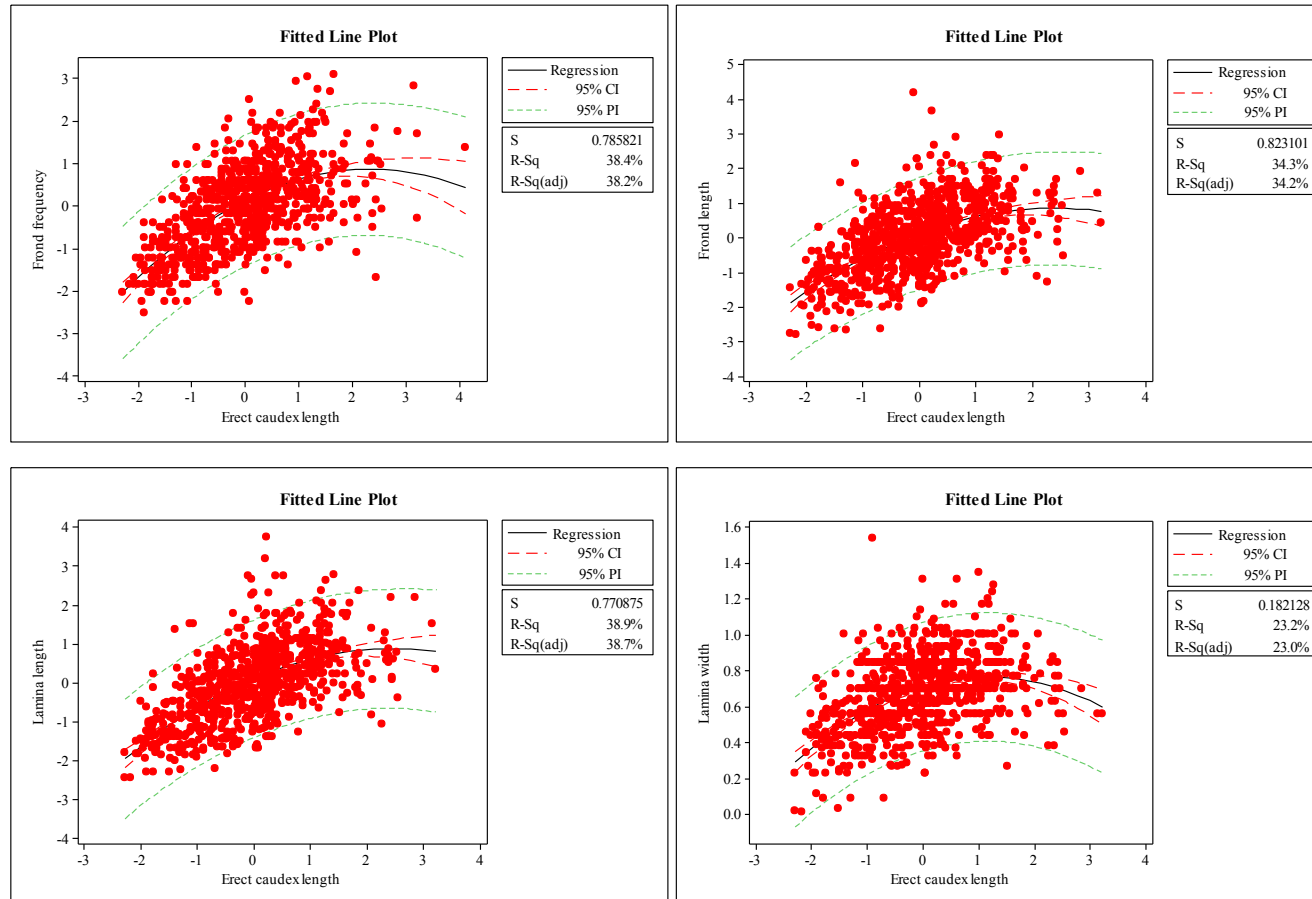


Figure 4.1 Fitted regression line plots of transformed *D. antarctica* morphological variables. Only those variables identified as possessing a significant relationship (α 0.05) by the regression analyses results in Table 3.1 are displayed. (CAI, crown area index).
Figure continued next page

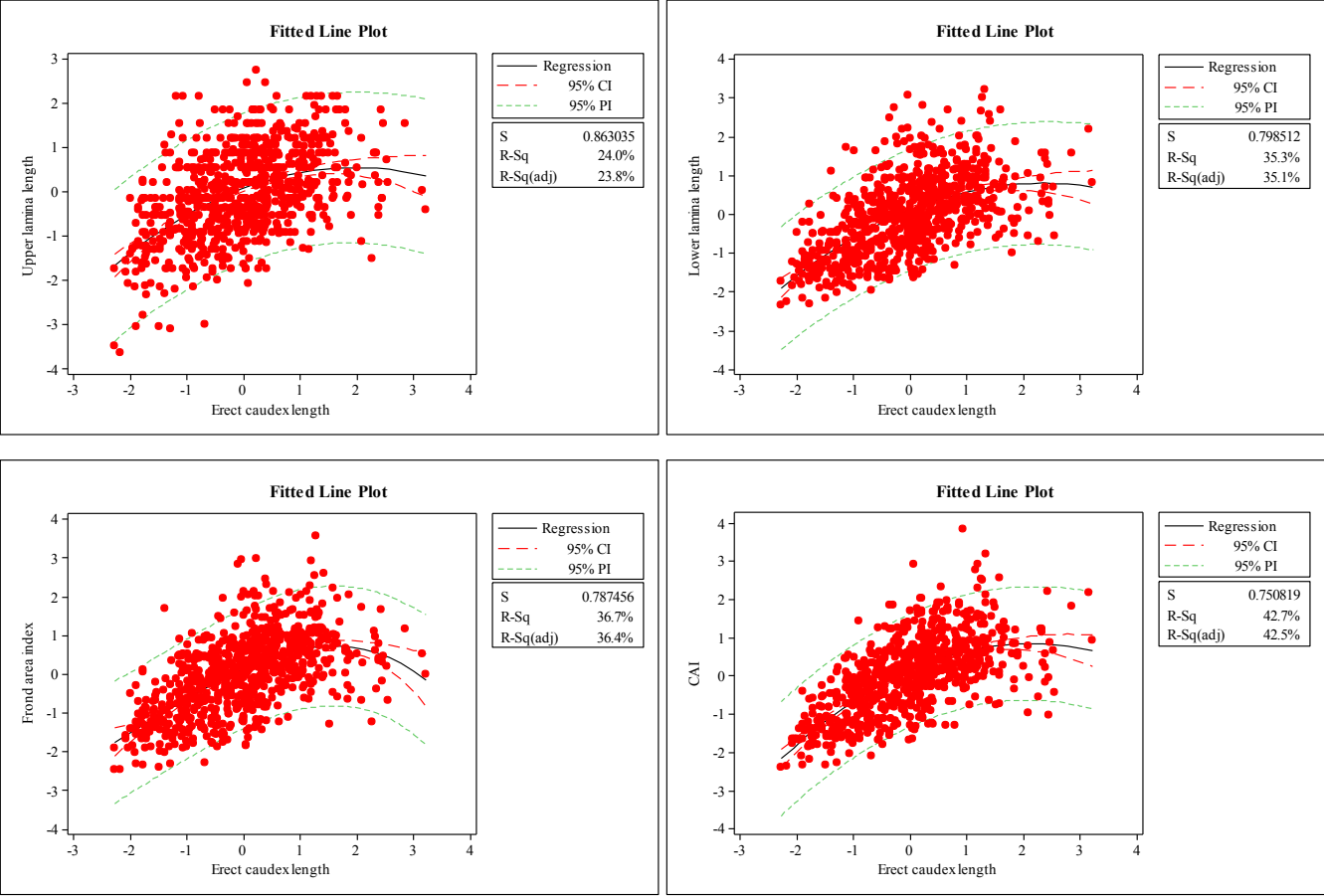


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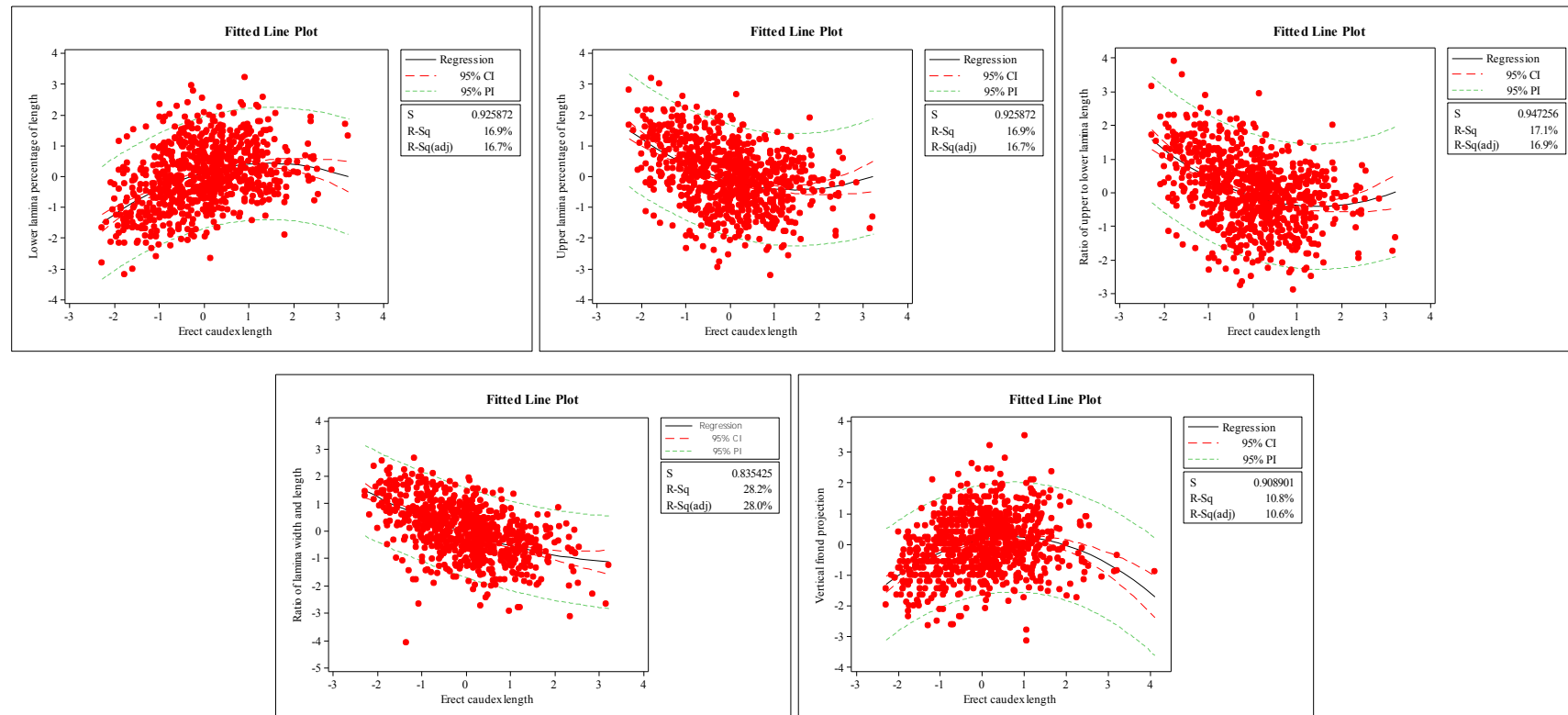


Figure 4.1 Final page

increase in ratio of lamina width and length between the two canopy closure classes (Appendix 1, Table 1.1).

The increase in frond size (represented by frond length, lamina width, lamina length, upper lamina length, lower lamina length and FAI) and frond frequency corresponds to an increase in site fertility from class 1 (low) to class 2 (high). However there is no change in the relative position of the maximum lamina width within the context of lamina length (represented by upper lamina percentage of length, lower lamina percentage of length, ratio of upper to lower lamina length, ratio of lamina width and length) between site fertility classes (Appendix 1, Table 1.1).

Only frond frequency increased from rainfall class 1 (low) to class 2 (high) (Appendix 1, Table 1.1). Lamina length from tip to maximum width and ratio of lamina width and length decreased from rainfall class 1 (low) to class 2 (Appendix 1, Table 1.1). All other frond variables did not vary between the two rainfall classes (Appendix 1, Table 1.1).

Maximum temperature and minimum temperature (as defined in Chapter 3) provided similar results. Frond length, lamina width, lamina length, upper lamina length and FAI decreased from maximum temperature class 1 (low) to class 2 (high) and from minimum temperature class 2 (high) to class 1 (low) (Appendix 1, Table 1.1). Upper lamina percentage of length, lower lamina percentage of length, ratio of upper to lower lamina length, ratio of lamina width and length remained unchanged among the classes of maximum temperature and minimum temperature (Appendix 1, Table 1.1). Lower lamina length remained unchanged among the temperature classes.

Discussion

Dicksonia antarctica erect caudex length, essentially equal to the height of the frond rosette above ground, increases with the growth and emergence of fronds from the apical meristem. Therefore, for a particular tree fern and a particular set of growing conditions, the

caudex length is generally representative of age, i.e. the longer the caudex the older the caudex (for the corresponding set of site conditions). The changes in frond size and frond frequency as well as frond shape as *D. antarctica* grow older and taller are revealed by the individual regressions of each frond morphological variable versus erect caudex length (Table 4.1 and Figure 4.1). It is likely that frond size (FAI, frond length, lamina length, lamina maximum width, upper lamina length and lower lamina length) and frequency will be dependant to a certain extent on the amount of resources allocated to frond production (as well as its genome, including a particular range attributable to phenotypic plasticity). Therefore it is reasonable to expect that a critical determinant of emerging frond size and frequency is the size of the *D. antarctica* photosynthate store as it is allocated towards frond production. Under ideal conditions *D. antarctica* will most likely attain an energy surplus each year with a consequently larger photosynthate store, which progressively leads in turn to the production of larger and more numerous fronds as the *D. antarctica* caudex increases in length (Figure 4.1). Consequently the observed relationship between caudex length and the size, frequency and shape of fronds is most likely an indirect one. Caudex length and the photosynthate storage are covariates and the direct relationship is between the photosynthate store and frond size and frond frequency.

The observed relationship of frond size and frequency with increasing caudex length is however not linear as they eventually plateau and then decrease at larger caudex lengths (i.e. essentially increased frond height from ground) (Figure 4.1). Since frond size and frequency are likely to be linked to the size of the photosynthate store then their reduction suggests the photosynthate store is undergoing a similar trend. One potential cause of this is the strong stomatal response of *D. antarctica* to VPD and a corresponding decrease in maximum net photosynthesis and quantum yield of photosynthesis with increasing VPD (Hunt *et al.* 2002). Vapour pressure deficit will tend to increase with height in the canopy due to an increasingly xeric microclimate and increased exposure (Givnish and Vermeij 1976). Consequently it can be expected when caudex apical growth positions the tree fern fronds at a height where VPD limits CO₂ uptake enough to significantly impact on

photosynthesis, then the photosynthate store will begin to plateau then decline with increasing caudex length, resulting in frond size and frequency following a similar trend which is evident in Figure 4.1. Although smaller and fewer fronds seem like a disadvantage as they have a smaller photosynthetic surface area, they transpire less (assuming stomatal density remains near constant). Provided water availability meets transpiration demand, photosynthate gain may equal the cost to produce fronds. This maybe the reason that frond size and frequency (and therefore possibly photosynthate store) progressively decline at the uppermost heights in the canopy (Figure 4.1). There is also an increasing per unit maintenance cost in supporting larger organs and tissues more distant from the substrate source.

The initial decline in the ratio of lamina width and length and the ratio of upper to lower lamina length with increasing caudex length (Figure 4.1) and height from ground indicate the lack of uniform growth in frond dimensions and the allocation of greater resources towards lamina length rather than lamina width and towards lower lamina length rather than upper lamina length. These trends could represent developmental variation as *D. antarctica* specimens age, i.e. allometric relationships, but other processes could be interfering with this. A similar trend is present between canopy closure class 1 and class 2 (Appendix 1, Table 1.1) where the ratio of lamina width and length increases with increasing canopy closure and decreasing light exposure and possibly decreasing VPD. Light exposure and VPD increase with height within the forest canopy (Givnish and Vermeij 1976) so the changes in ratio of upper to lower lamina length and ratio of lamina width and length with increasing height are potentially also showing adaptations of frond morphology to these conditions, i.e. phenotypic plasticity. If plasticity is the dominant influence, the plateau in the regression lines of the ratio of upper to lower lamina length and the ratio of lamina width and length (Figure 4.1) suggest VPD and light exposure are fairly constant. The reversal of this trend at the absolute end of the ratio of lamina width and length and the ratio of upper to lower lamina length regression plots could suggest a reversal of VPD and light exposure conditions. However, this is not necessarily the case since a greater degree of

uncertainty is present at the end of each regression line (Figure 4.1) due to the small number of extremely large *D. antarctica*.

Dicksonia antarctica caudices have the ability to survive falling over and even complete severing of their link to the soil (Hunt *et al.* 2002). Paradoxically falling over may reinvigorate a *D. antarctica* specimen if its apical frond rosette lands in a microclimate condition with suitable insolation and moisture. *Dicksonia antarctica* that have survived falling over are evident in the field by the presence of L shaped caudices, i.e. a horizontal section along the ground followed by an erect section representing growth since falling. The root mantle of the fallen caudex section eventually decays leaving the last vestiges of its rhizome as a trace merging with the base of the erect and alive caudex. The photosynthate store and fronds of a large fallen healthy *D. antarctica* should provide enough resources for it to root in the soil and to continue to produce fronds. According to the benefits of the new found microsite closer to the ground, and due to its larger photosynthate store and greater frond size and frequency the frond phenotype of large healthy fallen *D. antarctica* should reach a greater optimum compared to the young non-fallen *D. antarctica* of the same height from the ground. The smaller photosynthate store of young non-fallen *D. antarctica* will inhibit the size and frequency of fronds they can produce.

Light flecks can represent a significant source of sunlight (photosynthetically active radiation) absorbed by understorey species on a daily basis (Zhang *et al.* 2009). However, under dense canopies, such as in high canopy closure class 2, light fleck occurrence may be very limited or nonexistent leaving indirect (diffuse) light as the main source of light available to understorey species (Zhang *et al.* 2009). Modifying leaf form and frequency in response to varying light conditions enables many species to make efficient use of the available resource (Alves *et al.* 2004, Franklin *et al.* 2003, Givnish and Vermeij 1976). The reduction evident in *D. antarctica* frond length, lamina length, frond frequency and FAI with increasing canopy closure (Appendix 1, Table 1.1) and therefore decreasing available

sunlight can be expected when a resource, such as light, and the associated intra-plant photosynthate storage are limiting. Lamina width does contravene this trend by showing no reduction with increasing canopy closure, which is also evident in the increase in ratio of lamina width and length with increasing canopy closure (Appendix 1, Table 1.1). It can be reasoned that if longer fronds have the potential to intercept a greater frequency of sunflecks under a closed canopy where sunfleck frequency and duration are becoming limiting, the added risk of damage (by large falling debris) to long fronds may outweigh their photosynthetic benefit. In such conditions, a *D. antarctica* specimen that reduces its fronds' length but maintains frond width maximises the photosynthetic surface available to capture indirect light (with the resources available), but with a reduced likelihood of damage.

In addition to photosynthesis, *D. antarctica* fronds provide the additional functions of funnelling nutrients (in the form of litter debris) and rainfall to the caudex apex (Dearden and Wardle 2008, Hunt *et al.* 2002). Although frond length influences the effective diameter and hence area covered by the apical frond rosette (the funnel) of *D. antarctica*, it is lamina width that determines the likelihood of relatively small and fine debris (e.g. leaves and animal frass) being either directed to the fern's apex or falling sideways to the forest floor. Hence debris and water funnelling functions of the fronds may be maintained even though overall frond size decreases. The reduction of the ratio of upper to lower lamina length with increasing canopy closure (Appendix 1, Table 1.1), which signifies the reduction of upper lamina length proportionally more than lower lamina length, also indicates the maintenance of the fronds' water and debris funnelling function with increasing canopy closure and decreasing frond size. Especially in larger fronds, the laminar tip tends to curve over meaning the extension of upper lamina length is of less importance to effective debris and water collection. Increased frond length also increases the likelihood of frond overlap with other individuals, thereby reducing effective catchment area.

Dicksonia antarctica responds to increasing site fertility class with increased organ size and frond frequency, but not with a change in the relative proportion of frond dimensions (Appendix 1, Table 1.1). This does not necessarily imply that the largest *D. antarctica* occur on the more fertile sites as the fern is considerably long-lived, possibly exceeding 500 years (Mueck *et al.* 1996), and caudex erect length (essentially its height) increases with the growth and emergence of fronds from the apical meristem. Therefore growth may be slowed considerably if only a few small fronds emerge each year due to low site fertility or other unfavourable conditions. However, given added time (age) such *D. antarctica* can still reach considerable heights on less fertile sites. Consequently time since catastrophic disturbance and the frequency with which these occur at a site is potentially more important than soil fertility in determining the frequency of large, ageing *D. antarctica*. Adequate soil fertility, a moist microclimate (either high rainfall, riparian, or sheltered gully location) and optimal light (shade) condition are also important as these will increase growth rate which in turn will reduce the time needed between disturbances for large *D. antarctica* to develop.

In Tasmania's cool temperate rainforest, high soil fertility can even be a detriment to *D. antarctica* and other species occurring in the understorey of moist forests as it can lead to a dense *Nothofagus cunninghamii* overstorey that shades out or reduces the frequency of many understorey species including *D. antarctica* (Read 1995). The tendency of *D. antarctica* to form an apical debris ring, which is a source of nutrients (Dearden and Wardle 2008) may offset the effects of low soil fertility or low nutrient accessibility due to soil root competition. Thickness is probably an insufficient parameter on its own to determine the nutritional importance of the *D. antarctica* debris ring. For a complete understanding of the role of the apical debris ring, other variables that were not part of the current research must be taken into consideration. The following variables for example could hypothetically influence the type and amount of nutrients released from an apical debris ring: Nutrient content of debris, the tendency for the debris to decompose, the proportion of twigs versus leaves, ambient temperature, moisture level, as well as the presence and activity of arboreal browsers and decomposers.

Dicksonia antarctica has a strong stomatal response even to moderate vapour pressure deficit (VPD), and increasing VPD negatively affects maximum net photosynthesis and quantum yield of photosynthesis (Hunt *et al.* 2002). This is due to the stomatal response (i.e. closure) to high VPD limiting transpiration, and therefore water loss, but also limiting carbon uptake, resulting in reduced quantum yield of photosynthesis. Therefore prolonged exposure of *D. antarctica* to high VPD without access to adequate moisture will result in a photosynthate deficit. In situations of limited rainfall and soil water status *D. antarctica* would likely show a similar photosynthate deficit to that reported by Hunt *et al.* (2002) to occur in response to high VPD. A photosynthate deficit in *D. antarctica* should manifest in the form of smaller and fewer fronds. Consequently low rainfall sites should support *D. antarctica* with smaller and fewer fronds than *D. antarctica* supported by high rainfall sites. However, in the present study, only upper lamina length and ratio of lamina width and length increased from rainfall class 1 (low) to class 2 (high) (Appendix 1, Table 1.1). This lack of a response to varying rainfall, which hints at lamina width increasing at the expense of lamina length, may be due to site selection criteria focusing on large populations of mature *D. antarctica*, none of which occurs at sufficiently low rainfall sites, i.e. an insufficient sample of tree fern populations existed at sites receiving an average rainfall less than 1000 mm/year.

Wider fronds in *D. antarctica* may not necessarily result in greater water collection per frond compared to narrower fronds because the edges of fronds tend to curve downwards. Therefore the farther away from the central axis or rachis that rain impacts the frond, the less likely the water will flow down the rachis to the caudex apex, but instead will flow over its edge. Therefore the apparent reduction in lamina length relative to lamina width (ratio of lamina width and length, Appendix 1, Table 1.1) with increasing rainfall class suggests an advantage gained by reducing water collection in areas of high rainfall. One benefit to *D. antarctica* of reduced water collection in areas of high rainfall is to avoid saturation of the apical meristem which may lead to it rotting. On the other hand frond frequency increases with increasing rainfall class 1 (low) to class 2 (high) (Appendix 1,

Table 1.1). A greater frond frequency with no change in FAI (Frond Area Index) typically means a greater transpiration rate and an increased water demand (Givnish and Vermeij 1976). The higher rainfall of class 2 (high) compared to class 1 (low) (Appendix 1, Table 1.1) may enable *D. antarctica* to produce a greater frequency of fronds. However, a greater frequency of live fronds would tend to lead to greater volume of water funnelled to the caudex.

Temperature of the forest environment possesses a strong influence on plant life. Evaporation and VPD and therefore water availability and the water demand of a plant are influenced by air temperature. The rates of chemical reactions critical for photosynthesis in plants are also temperature dependant (Givnish and Vermeij 1976) and extremes of temperature can result in plant tissue damage and death and for high temperature, productivity losses due to photorespiration (Monneveux *et al.* 2003). Maximum temperature and minimum temperature can be taken as broadly indicative of the high and low temperature extremes experienced at a site. The greater extreme (maximum temperature class 2 and minimum temperature class 1), the greater the likelihood of conditions occurring that are detrimental to *D. antarctica* condition and productivity. The declining frond size and frequency with increasing maximum temperature (Appendix 1, Table 1.1) could be due to a declining photosynthate store. High temperatures can lead to a high VPD and VPD has a negative effect on the quantum yield of photosynthesis (Hunt *et al.* 2002) and therefore the photosynthate store, causing the next generation of fronds to be fewer and smaller. This next generation of smaller and fewer fronds will transpire less (all else being equal) compared to the older fronds, thereby potentially reducing water demand. Low temperature extremes have a similar reducing affect on *D. antarctica* frond size and frequency as high temperature extremes (Appendix 1, Table 1.1). High VPD is probably not the culprit, but slowing of temperature dependant photosynthetic reactions leading to reduced photoassimilation and a corresponding smaller photosynthate store could be the cause. Another hypothesis is that the photosynthate store is being depleted seasonally to replace croziers burnt off by frost, leading to replacement fronds being smaller and fewer.

Conclusion

Although regression analysis supports the hypothesis that frond size, shape and frequency are dependent on caudex length (Table 4.1 and Figure 4.1), the relationship is potentially indirect. Instead it is likely that frond size and frequency are influenced by the allocation of resources to frond production, which is in turn influenced by the size of the photosynthate store. The caudex length and the photosynthate store are therefore covariates since both will tend to increase as *D. antarctica* matures. Differing leaf size and morphology with height in the canopy is a common phenomenon in plants (Givnish and Vermeij 1976). However, in the case of forest trees, differing leaf size is typically a plastic response of leaves at differing heights on the same plant, whereas *D. antarctica* positions all its fronds at approximately the same height within the one plant. Differing frond size and form is more likely among individuals of different caudex lengths.

The negative relationships of the ratio of lamina width and length and the ratio of upper to lower lamina length with increasing erect caudex length (Figure 4.1) are potentially a plastic response to increasing light and xeric conditions with increasing height in the canopy. Supporting this is the increase in ratio of lamina width and length from canopy closure class 1 (low) to class 2 (low) i.e. with decreasing light and possibly increasing VPD. Except for lamina width, which is static, frond size and frond frequency decrease with increasing canopy closure (Appendix 1 Table 1.1) potentially due to the lower light levels under a denser canopy. Preserving lamina width at the expense of other frond dimensions under conditions of decreasing light and possibly increasing VPD could help to maximise photosynthetic surface area as well as maintain the frond's debris and water collecting functions.

Dicksonia antarctica photosynthesis can be restricted at high VPD (Hunt *et al.* 2002) which can be exacerbated by low water availability. Therefore any variable that influences either water availability or water demand could elicit a plastic response in *D. antarctica* fronds. Maximum temperature and rainfall are two environmental variables that can influence

VPD, water availability and water demand, but only maximum temperature was associated with a definite difference in frond size and frequency. The reduction in frond size and frequency with increasing maximum temperature may not be plasticity (through acclimation), but could instead be due to high VPD at high temperatures leading to a reduction in the fern's photosynthate storage and the allocation of resources to frond production. All else being equal the resulting smaller and fewer fronds should transpire less thereby reducing water demand and the impact of high VPD on *D. antarctica*.

The hypotheses that frond size and frequency have a positive association with rainfall of the sites was not supported by the results of analysis. A possible reason for this is moisture available to *D. antarctica* is not only determined by average annual rainfall, but also by drainage and evaporation, the latter is influenced by temperature, light intensity and wind speed which also affect VPD. Stemflow down through the caudex is a critical moisture source for *D. antarctica* as there are adventitious roots at the base of fronds and within the caudex. An apical debris ring and its marcescent fronds will lower evaporation from the upper caudex, meaning they also influence moisture loss from stem storage in the region closest to maximum growth activity. Therefore rainfall class and temperature class alone are insufficient to determine if *D. antarctica* frond size, frequency and morphology varies with changing water availability and water demand.

Chapter 5: *Dicksonia antarctica* as a substrate for obligate epiphytes

Introduction

In the context of canopy biology an epiphyte is a plant that is reliant upon another plant for mechanical support and does not actively extract nutrients or water from the living host tissue, i.e. it is not a parasite, and does not have root connections to the ground (Debenham 1971, Moffett 2000). Epiphytism grades into the soil rooted habit (Zotz 2005) with vascular epiphytes categorised into four groups: obligate epiphytes which occur predominantly as epiphytes, hemi-epiphytes in which only part of their lifecycle is as an epiphyte with the remainder rooted in the ground, facultative epiphytes which can germinate and reproduce as either an epiphyte or when rooted in the ground, and accidental epiphytes which can occur as but are not reproductively successful as epiphytes (Debenham 1971, Moffett 2000, Nieder and Barthlott 2001). Hemi-epiphytes can be divided into two types: primary, which germinate in the canopy and become rooted in the soil, and secondary, which germinate on the ground, grow onto a host tree and eventually lose their connection with the soil. The epiphytes' environment is typically characterised by high light availability, but also extreme variation in temperature, moisture availability, and nutrient availability that can make conditions very harsh (Huston 1994). Obligate and hemi-epiphytes generally have specific adaptations to enhance their survival in this environment (Benzing 2008). Facultative and accidental epiphytes tend not to possess specific adaptations to the epiphytic habit and therefore occur in their greatest frequency and diversity where canopy and terrestrial conditions are similar (Benzing 2008).

Tasmania contains the largest expanse of cool temperate rainforest in Australia as well as large areas of wet sclerophyll and mixed (rainforest/eucalypt) forest. The majority of Tasmania's vascular obligate epiphytes (henceforth referred to as obligate epiphytes) are pteridophytes and occur predominantly within wet forest, with several able to colonise

multiple host species (Garrett 1996b). Compared to tropical latitudes, Tasmania's obligate epiphyte diversity, in common with other temperate latitudes, is depauperate (Huston 1994, Schulze *et al.* 2005, Zotz 2005). This may be due to a number of reasons such as low temperatures, a relatively small diversity of large long-lived tree species, the high incidence of fire in much of Tasmania's vegetation (including wet forests), as well as population fragmentation and extinction during Pleistocene glaciations (Zotz 2005).

In Tasmania's wet forests *D. antarctica* is a major obligate epiphyte host with 12 species known to colonise it (Garrett 1996b). The *D. antarctica* caudex differs from other hosts, that are tree species, by providing a moisture retentive substrate relatively close to the ground (0 to 12 m height). The caudex of *D. antarctica* varies in texture and structure with the majority of the lower section composed of a fibrous root mantle that forms a continuum with the soil. The root mantle is considered to be an ideal rooting medium for plant species, evident by the large number of typically terrestrial species (i.e. species with no or limited epiphytic adaptations) that have been observed to colonise it (Garrett 1996b, Ough and Ross 1992).

Globally many obligate epiphyte species have adapted to specific structures of their host(s). *Tillandsia eistetteri* Ehlers for example is predominantly associated with outer branches (Reyes-García *et al.* 2008), while *Tillandsia multicaulis* Steud. prefers heavier shadier branches (Hietz *et al.* 2002, Reyes-García *et al.* 2008). The obligate epiphytes of *D. antarctica* could also be associated with specific features of its caudex and fronds. Hydrophilic epiphyte species, for instance, could be expected to be associated with the lower more sheltered and moisture retentive sections of the *D. antarctica* caudex. Other epiphyte species more tolerant of xeric conditions could be expected to be associated with the more exposed sections of the caudex, toward the fern's apex.

Based on this reasoning this chapter will test the hypotheses that:

- Epiphyte frequency and epiphyte species richness are positively associated with those parts of the caudex facing either a southern or eastern aspect, as in southern latitudes these provide a more sheltered microclimate for epiphytes than northern or western aspects;
- Epiphytes occur at greater heights on those parts of the caudex facing either a southern or eastern aspect as these provide a microclimate, which is more sheltered from the wind and sun and that is higher on the caudex compared to either the northern or western aspects;
- The caudex frequency of filmy ferns (*Hymenophyllum* spp. and *Crepidomanes venosum* (R.Br.) Bostock), *Asplenium bulbiferum*, *Grammitis billardiarei* and *Tmesipteris obliqua* Chinnock and caudex epiphyte species richness are positively associated with the “rough” textured surface of the *D. antarctica* caudex. This section of the caudex is thicker, moisture retentive and more sheltered than other sections of the caudex, which makes it ideal for epiphyte colonisation, especially filmy ferns. The other species of epiphyte tend to occur on the lower caudex and could be expected to benefit from the moist microclimate. It is also the oldest section of the tree fern, which should provide more time for epiphyte colonisation;
- *Microsorium pustulatum* (G.Forst.) Copel. and *Rumohra adiantiformis* (G.Forst.) Ching are positively associated with the “fuzzy” textured surface of the *D. antarctica* caudex. This texture occurs toward the tree fern’s apex, which is where these two species are observed to occur; and
- Caudex epiphyte frequency (for each species) and caudex epiphyte species richness are positively associated with *D. antarctica* frond frequency and frond size. Larger more numerous fronds should provide an increasingly sheltered microclimate conducive to the epiphyte species of the lower *D. antarctica* caudex.

Since several species of epiphyte, e.g. filmy ferns, appear to occur more frequently on the lower *D. antarctica* caudex, which tends to be the more sheltered and moisture retentive

part of the caudex, it is possible that general site variations in maximum temperature, rainfall and canopy closure will affect epiphyte species frequency. Based on this reasoning this chapter will also test the hypotheses that:

- Epiphyte frequency and epiphyte species richness are positively associated with canopy closure and rainfall (mean annual rainfall) of the site as these two variables will augment the moist sheltered microclimate of the lower caudex; and
- Epiphyte frequency and epiphyte species richness are negatively associated with maximum air temperature (as defined in Chapter 3) as increasing temperature will increase the desiccation risk to epiphytes.

This chapter will also test the hypothesis that epiphyte frequencies and epiphyte species richness are dependent on the density of *D. antarctica* caudices. The reasoning behind this hypothesis is that the greater the frequency of *D. antarctica* caudices the more niche space is available for epiphyte colonisation.

Only those obligate epiphyte species identified to possess sufficient frequency and distribution across the field sites were included in this analysis, namely *Asplenium bulbiferum*, *Crepidomanes venosum*, *Grammitis billardiarei*, *Hymenophyllum flabellatum*, *Hymenophyllum rarum* R.Br., *Microsorium pustulatum*, *Rumohra adiantiformis* and *Tmesipteris obliqua*. The remaining obligate epiphyte species, i.e. *Hymenophyllum australe*, *Hymenophyllum cupressiforme* Labill. and *Hymenophyllum peltatum* (Poir.) Desv. were excluded from analysis as they occurred in only one site each.

Analysis

The abundance measures of obligate epiphyte species, *D. antarctica* morphological variables and environmental classes recorded in or attributed to the study plots described in Chapter 3 (Site Selection and Field Sampling) were also used in this analysis. Refer to Chapter 3 for details of site selection and field sampling.

The fitted line plot regression analysis ($\alpha \leq 0.05$) (MINITAB 2005) was used to test the hypothesis that epiphyte species frequencies and epiphyte species richness are dependent on *D. antarctica* caudex density. Variables were transformed to meet the assumptions of regression analysis where possible. The regression fitted line plot produced by MINITAB was used to display significant relationships. For those epiphyte species whose site frequencies could not be transformed, the Spearman's Rank Correlation ($\alpha \leq 0.05$) (MINITAB 2005) was used.

Analysis of variance using the General Linear Model (ANOVA) ($\alpha 0.05$) (MINITAB 2005) was used to test the following hypotheses:

- Epiphyte frequency and epiphyte species richness are positively associated with canopy closure and rainfall (mean annual rainfall) of the site; and
- Epiphyte frequency and epiphyte species richness are negatively associated with maximum temperature (as defined in Chapter 3).

Each environmental class (canopy closure, site fertility, rainfall and maximum temperature) consists of two values with class 1 lower than class 2 (as outlined in Chapter 3). All of the environmental variables were included in each ANOVA model. The site caudex density was selected as a covariate where appropriate to remove background variability caused by differing substrate availability between sites. If a factor was identified by ANOVA as being non-significant then that factor/s was/were removed and the model recalculated. The Tukey test provided as part of the ANOVA option in MINITAB was used to determine the difference between each significant factor's class. When necessary the variables were transformed to meet the assumptions of ANOVA where possible. For those epiphyte frequencies that could not be transformed (*Asplenium bulbiferum*, *Hymenophyllum rarum* and *Tmesipteris obliqua*) to meet the assumptions of ANOVA the Kruskal-Wallis test ($\alpha 0.05$) (MINITAB 2005) was used as the non-parametric alternative.

Changes in epiphyte frequency (Table 5.4) as well as *D. antarctica* frond size, frond frequency and caudex dimensions (Appendix Table 1.1) are associated with *D. antarctica*

caudex erect length. Correlation of these variables with *D. antarctica* caudex erect length will therefore cloud the relationship between epiphyte frequency and the *D. antarctica* morphological variables, i.e. by autocorrelation. To remedy this, *D. antarctica* caudex erect length was regressed (using the fitted line plot regression analysis (α 0.05) (MINITAB 2005)) with those *D. antarctica* variables shown to be associated with it (Appendix Table 1.1) and the residual variation stored. The residual variation represents the variation in each of the *D. antarctica* morphological variables that is not explained by *D. antarctica* erect caudex length. The residual variation of each *D. antarctica* morphological variable was then ranked as was each epiphyte species' frequency. The Spearman's rank correlation (α 0.05) (MINITAB 2005) was then used to test the hypothesis that:

- Caudex epiphyte frequency (for each species) and caudex epiphyte species richness are positively associated with *D. antarctica* frond frequency and frond size.

ANOVA (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- Epiphytes occur at greater heights on those parts of the caudex facing either a southern or eastern aspect.

The Tukey test provided as part of the ANOVA option in MINITAB (2005) was used to determine if a significant variation occurred in epiphyte species' height between aspect classes. For those epiphyte frequencies that could not be transformed (*Hymenophyllum rarum* and *Microsorium pustulatum*) to meet the assumptions of ANOVA the Kruskal-Wallis test (α 0.05) (MINITAB 2005) was used.

The Kruskal-Wallis Test (α 0.05) (MINITAB 2005) was used to test the following hypotheses:

- Epiphyte frequency and epiphyte species richness are positively associated with those parts of the caudex facing either a southern or eastern aspect;
- The caudex frequency of filmy ferns (*Hymenophyllum* spp. and *Crepidomanes venosum* (R.Br.) Bostock), *Asplenium bulbiferum*, *Grammitis billardiarei* and *Tmesipteris obliqua*

Chinnock and caudex epiphyte species richness are positively associated with the “rough” textured surface of the *D. antarctica* caudex; and

- *Microsorium pustulatum* (G.Forst.) Copel. and *Rumohra adiantiformis* (G.Forst.) Ching are positively associated with the “frizzy” textured surface of the *D. antarctica* caudex.

Since aspect and texture are multi-class variables, when a significant variation was initially identified, individual Kruskal-Wallis Tests were conducted among each combination of classes to identify between which classes the significant variation was identified.

ANOVA (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- The attachment height of mature *Asplenium bulbiferum* and *Grammitis billardiarei* on *D. antarctica* caudices is greater than the attachment height of immature *Asplenium bulbiferum* and *Grammitis billardiarei*.

The Tukey test provided as part of the ANOVA option in MINITAB (2005) was used to determine the difference in attachment height among the classes of immature vs. mature epiphytes. For those epiphyte attachment heights that could not be transformed to meet the assumptions of ANOVA the Kruskal-Wallis test (α 0.05) (MINITAB 2005) was used.

Results

Eleven species of obligate epiphyte were identified as being rooted in *D. antarctica* caudices and all these are members of Division Pteridophyta (Table 5.1). Eight species were identified to possess sufficient frequency and distribution to be suitable for data analysis here (as outlined in Chapter 3). These were *Asplenium bulbiferum*, *Crepidomanes venosum*, *Grammitis billardiarei*, *Hymenophyllum flabellatum*, *Hymenophyllum rarum*, *Microsorium pustulatum*, *Rumohra adiantiformis* and *Tmesipteris obliqua* (Table 5.1). One large specimen of *Huperzia varia* (R.Br.) Trevis. (Lycopodiaceae) was identified growing approximately 1.3 metres up a *D. antarctica* caudex, but occurred outside the sample quadrat. In addition, the angiosperm obligate epiphyte *Sarcochilus australis* (Lindl.) Rchb.f. (Family Orchidaceae) was identified within two sample sites, but was observed in

both instances to be hosted by the outer branches of very large (and presumably old)

Coprosma quadrifida (Labill.) B.L.Rob.

Table 5.1 Epiphyte species identified as growing on *D. antarctica* caudices. The _common epiphyte_ species are marked (*). The total frequency of species notated (1) correspond to the number of sub-caudex quadrats each species (when cover is > 25 %) occurs in across all caudices.

Species	Family	Total Frequency	Height on Caudex (m)		
			Min	Mean	Max
<i>Asplenium bulbiferum</i> *	Aspleniaceae	1010	0.00	1.03	4.33
<i>Crepidomanes venosum</i> * ¹	Hymenophyllaceae	2225	0.00	1.40	6.50
<i>Grammitis billardiarei</i> *	Grammitidaceae	1198	0.00	0.81	5.50
<i>Hymenophyllum australe</i> ¹	Hymenophyllaceae	59	0.00	1.97	5.50
<i>Hymenophyllum cupressiforme</i> ¹	Hymenophyllaceae	4	0.00	0.12	0.49
<i>Hymenophyllum flabellatum</i> * ¹	Hymenophyllaceae	484	0.00	1.09	5.50
<i>Hymenophyllum peltatum</i> ¹	Hymenophyllaceae	1	-	0.46	-
<i>Hymenophyllum rarum</i> * ¹	Hymenophyllaceae	170	0.00	1.18	5.50
All Hymenophyllaceae	Hymenophyllaceae	2943	0.00	1.35	6.50
<i>Microsorium pustulatum</i> * ¹	Polypodiaceae	892	0.00	1.62	7.50
<i>Rumohra adiantiformis</i> * ¹	Dryopteridaceae	715	0.00	2.65	7.00
<i>Tmesipteris obliqua</i> *	Psilotaceae	65	0.13	1.33	5.00

Approximately 50 % of variations in site by site frequencies of *Crepidomanes venosum*, *Microsorium pustulatum* and *Rumohra adiantiformis* were explained by site caudex density using the regression analysis (Table 5.2). Twenty five percent of variation in site species richness was explained by site caudex density (Table 5.2). The respective relationships of site by site frequencies of *Microsorium pustulatum*, *Rumohra adiantiformis* and species richness with site caudex density were best expressed as linear equations (Figure 5.1). The relationship of site by site frequencies of *Crepidomanes venosum* with site caudex density was non-linear (Figure 5.1). However, the outlying position of a single isolated data point at the left hand side of the fitted line plot may be disproportionally influencing the regression line of *Crepidomanes venosum* frequency (Figure 5.1).

Frequency of *Asplenium bulbiferum* was the only variable identified to be correlated with tree fern caudex density (Table 5.2). Respective frequencies of *Grammitis billardiarei*, *Hymenophyllum flabellatum*, *Hymenophyllum rarum* and *Tmesipteris obliqua* at each site were not related significantly with tree fern caudex density (Table 5.2).

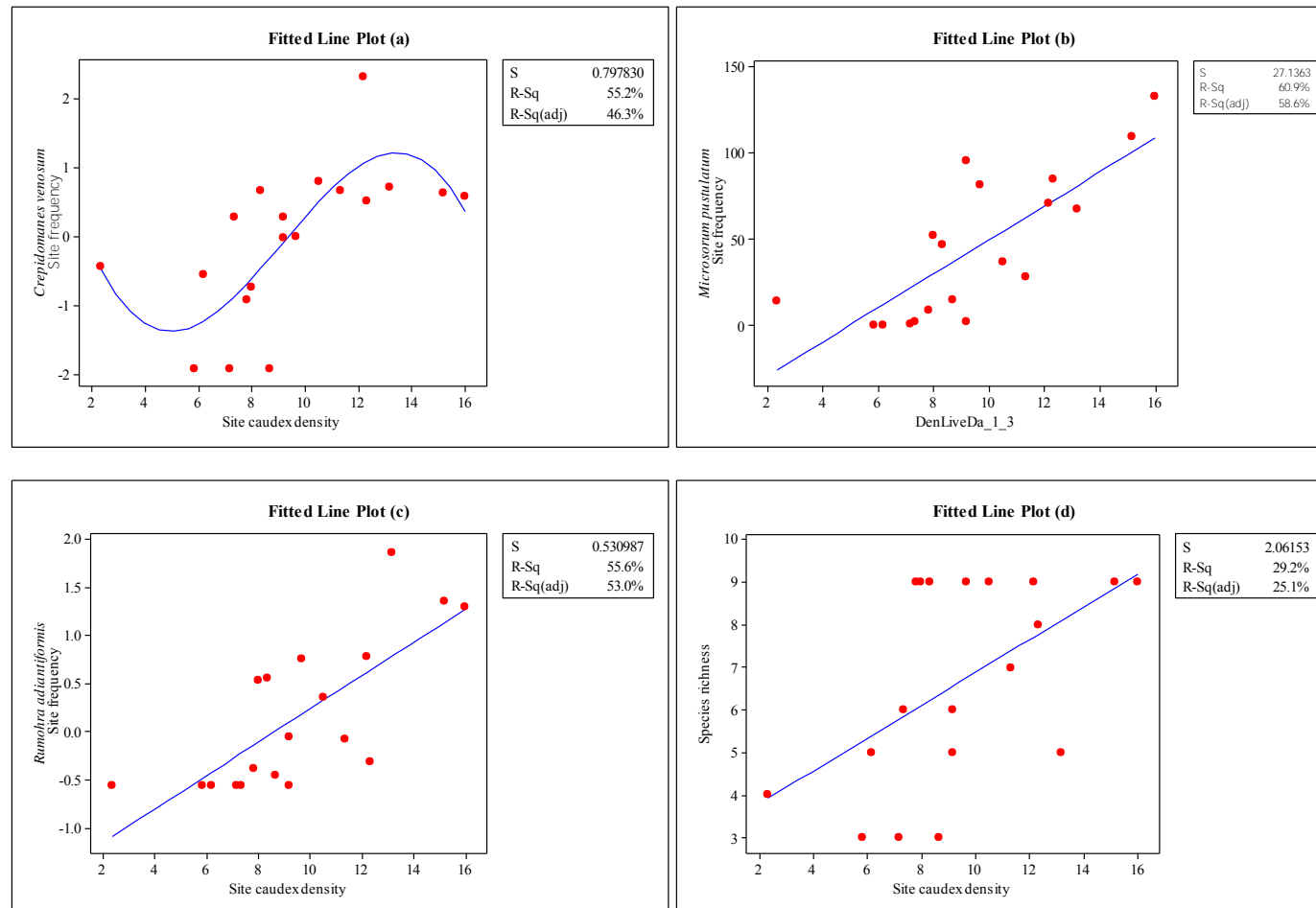


Figure 5.1 Fitted regression line plots of (a) *Crepidomanes venosum* frequency (transformed), (b) *Microsorium pustulatum* frequency, (c) *Rumohra adiantiformis* frequency (transformed) and (d) obligate epiphyte species richness versus caudex density (transformed). Only those variables identified as possessing a significant relationship by the regression analyses results in Table 5.2 are displayed.

Table 5.2 Results of regression analyses ($\alpha \leq 0.05$) (R^2 Adj) of epiphyte species frequency versus site caudex density. The table includes the results of the Spearman's rank correlation (r) of those variables not meeting the assumptions of regression analysis. (***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$; ns, not significant; na, not applicable).

Frequency	R^2 Adj	r
<i>Asplenium bulbiferum</i>	na	0.735 ***
<i>Crepidomanes venosum</i>	46.3 % **	na
<i>Grammitis billardierei</i>	ns	na
<i>Hymenophyllum flabellatum</i>	ns	na
<i>Hymenophyllum rarum</i>	na	ns
<i>Microsorium pustulatum</i>	58.6 % ***	na
<i>Rumohra adiantiformis</i>	53.0 % ***	na
<i>Tmesipteris obliqua</i>	na	ns
Total Frequency (All Species)	65.9 % *	na
Species Richness	25.1 % *	na

The site frequencies of *Asplenium bulbiferum*, *Crepidomanes venosum*, *Grammitis billardierei*, *Hymenophyllum flabellatum*, *Hymenophyllum rarum* and site species richness all displayed a negative association with maximum temperature (Table 5.3 and Appendix 2, Table 2.1). *Hymenophyllum rarum* frequency displayed a positive association with canopy closure (Table 5.3). *Microsorium pustulatum* frequency displayed a significant negative association with canopy height (Appendix 2, Table 2.1). *Tmesipteris obliqua* frequency displayed a significant negative association with site fertility class (Table 5.3 and Appendix 2, Table 2.1).

Table 5.3 Results of separate Kruskal-Wallis tests ($\alpha \leq 0.05$). Response: Site epiphyte species frequency, Factors: Canopy closure, rainfall, maximum temperature, canopy height and site fertility. The number in brackets indicates which class has the greater average rank of the two. (*, $p \leq 0.05$; ns, not significant).

Environmental Variable	Species		
	<i>Asplenium bulbiferum</i>	<i>Hymenophyllum rarum</i>	<i>Tmesipteris obliqua</i>
Site fertility	ns	ns	(1) 4.24*
Rainfall	ns	ns	ns
Maximum temperature	(1) 3.86 *	(1) 14.63*	ns
Canopy closure	ns	(2) 5.98*	ns
Canopy height	ns	ns	ns

All epiphyte species frequencies except for *Tmesipteris obliqua*, plus caudex species richness displayed a significant positive correlation with caudex erect length (Table 5.4). Frequencies of *Crepidomanes venosum*, *Grammitis billardierei*, *Hymenophyllum flabellatum* and *Microsorium pustulatum* on *D. antarctica* caudices and species richness on *D. antarctica* caudices also displayed a significant positive correlation with the length of the caudex classed as being of a rough texture (Table 5.4 and Figure 3.1).

Only *Asplenium bulbiferum* frequency displayed a relationship with the length of the caudex classed as being of an irregular texture, this being a weak negative correlation (Table 5.4 and Figure 3.1). Frequency of *Asplenium bulbiferum* on the tree fern caudex displayed a weak positive correlation with the length of the caudex classed as being of a frizzy texture (Table 5.4 and Figure 3.1). *Grammitis billardierei* caudex frequency displayed a weak negative correlation with the length of the caudex classed as being of a frizzy texture (Table 5.4 and Figure 3.1). Frequency of *Crepidomanes venosum* on tree fern caudices displayed a weak negative correlation with the maximum diameter of the caudex (Table 5.4). *Asplenium bulbiferum* caudex frequency displayed a weak correlation with frond size and with the frond frequency variables, except for lamina width and residual frond frequency (Table 5.4). *Crepidomanes venosum*, *Grammitis billardierei*, *Hymenophyllum flabellatum* and *Hymenophyllum rarum* caudex frequencies and caudex species richness displayed a slight negative correlation with residual frond frequency (Table 5.4). *Crepidomanes venosum* caudex frequency displayed a weak positive correlation with lamina width and frond area index (Table 5.4). Caudex species richness also displayed a weak positive correlation with lamina width (Table 5.4). The frequency of all species on the tree fern caudex (except for *Hymenophyllum rarum* and *Tmesipteris obliqua*) and caudex species richness displayed a weak correlation with debris ring length (Table 5.4).

Table 5.4 Results of Spearman's Rank Correlation ($\alpha \leq 0.05$) of species frequency versus *D. antarctica* caudex and frond variables. Debris ring length is the length of the caudex occupied by the debris ring. (***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$; ns, not significant; RCT, rough caudex texture; ICT, irregular caudex texture; FCT, frizzy caudex texture).

Frequency	<i>D. antarctica</i> variables										
	Erect caudex length	RCT	ICT	FCT	Max diameter	Frond frequency	Residual frond frequency	Frond length	Lamina width	FAI	Debris ring length
<i>Asplenium bulbiferum</i>	0.405 ***	ns	-0.072 *	0.096 ***	ns	0.075 *	ns	0.075 *	ns	0.113 ***	-0.188 ***
<i>Crepidomanes venosum</i>	0.565 ***	0.125 ***	ns	ns	-0.093 ***	ns	-0.154 ***	ns	0.076 *	0.111 ***	-0.249 ***
<i>Grammitis billardierei</i>	0.287 ***	0.072 *	ns	-0.097 ***	ns	ns	-0.071 *	ns	ns	ns	-0.119 ***
<i>Hymenophyllum flabellatum</i>	0.277 ***	0.093 ***	ns	ns	ns	ns	-0.087 **	ns	ns	ns	-0.094 ***
<i>Hymenophyllum rarum</i>	0.125 ***	ns	ns	ns	ns	ns	-0.068 *	ns	ns	ns	ns
<i>Microsorium pustulatum</i>	0.359 ***	0.065 *	ns	ns	ns	ns	ns	ns	ns	ns	-0.143 ***
<i>Rumohra adiantiformis</i>	0.436 ***	ns	ns	ns	ns	ns	ns	ns	ns	ns	-0.224 ***
<i>Tmesipteris obliqua</i>	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Species richness	0.637 ***	0.167 ***	ns	ns	ns	ns	-0.131 ***	ns	0.077 *	ns	-0.260 ***

Grammitis billardierei was the sole species in which its height on the caudex showed significant variation among the aspect classes (Table 5.5 and Table 5.6). No significant variation occurred between the height of *Grammitis billardierei* on *D. antarctica* caudices in aspect classes 1 (North) and 4 (West), and between those in classes 2 (East) and 3 (South) (Table 5.5).

There was no significant variation between *Crepidomanes venosum* frequency in aspect classes 1 (North) and 4 (West) and between those in aspect classes 2 (East) and 3 (South) (Table 5.5). The frequency of *Hymenophyllum rarum* displayed an almost identical pattern to *Crepidomanes venosum* except for aspect classes 3 (South) and 4 (West) which displayed no significant variation between them (Table 5.5). *Hymenophyllum flabellatum* frequencies displayed limited differentiation with aspect as only classes 1 (North) and 3 (South) were identified as different (Table 5.5). The frequencies of *Asplenium bulbiferum*, *Grammitis billardierei*, *Microsorium pustulatum*, *Rumohra adiantiformis* and *Tmesipteris obliqua* displayed no significant variation between aspect classes (Table 5.5).

The greatest frequencies of *Asplenium bulbiferum*, *Crepidomanes venosum*, *Grammitis billardierei*, *Hymenophyllum flabellatum* and *Hymenophyllum rarum* occurred on the section of caudex with a rough texture (Class 1) (Table 5.5). Both *Microsorium pustulatum* and *Rumohra adiantiformis* occurred at their greatest frequencies on the section of caudex with a frizzy texture (Class 3) (Table 5.5). *Tmesipteris obliqua* occurred only on the sections of the caudex with a rough or irregular texture (class 1 and 2 respectively) with no significant variation between the frequency of these two classes (Table 5.5 and Figure 5.2).

Table 5.5 Results of ANOVA ($\alpha \leq 0.05$). Response: Height on caudex of species, Factor: Aspect of caudex individual occupies on caudex (4 classes, 1 = North, 2 = East, 3 = South, 4 = West); Response: Height on caudex of species, Factor: growth stage of epiphyte (2 classes, 1 = immature, 2 = mature) (***, $p \leq 0.001$; **, $p \leq 0.01$; ns, not significant; na, not applicable).

Species	Response	Model Components		F	R ² (adj)	Class with greater mean identified by Tukey test					
		Type	Variable			2 - 1	3 - 1	4 - 1	3 - 2	4 - 2	4 - 3
<i>Asplenium bulbiferum</i>	Height on caudex	Covariate	Erect caudex length	226.62 ***	ns	ns	ns	ns	ns	ns	ns
		Factor	Aspect	0.91 ns							
<i>Crepidomanes venosum</i>	Height on caudex	Covariate	Erect caudex length	507.10 ***	ns	ns	ns	ns	ns	ns	ns
		Factor	Aspect	0.44 ns							
<i>Grammitis billardierei</i>	Height on caudex	Covariate	Erect caudex length	309.25 ***	27.83 %	1 ***	1 ***	ns	ns	4 **	4 ***
		Factor	Aspect	16.29 ***							
<i>Hymenophyllum flabellatum</i>	Height on caudex	Covariate	Erect caudex length	58.89 ***	ns	ns	ns	ns	ns	ns	ns
		Factor	Aspect	1.39 ns							
<i>Rumohra adiantiformis</i>	Height on caudex	Covariate	Erect caudex length	325.69 ***	ns	ns	ns	ns	ns	ns	ns
		Factor	Aspect	0.43 ns							
<i>Tmesipteris obliqua</i>	Height on caudex	Covariate	Erect caudex length	126.29 ***	ns	ns	ns	ns	ns	ns	ns
		Factor	Aspect	0.76 ns							
<i>Asplenium bulbiferum</i>	Height on Caudex	Covariate	Erect caudex length	216.67 ***	26.29 %	2 ***	na	na	na	na	na
		Factor	Growth stage	66.37 ***							
<i>Grammitis billardierei</i>	Height on Caudex	Covariate	Erect caudex length	368.12 ***	ns	ns	na	na	na	na	na
		Factor	Growth stage	2.81 ns							

Table 5.6 Results of Kruskal-Wallis tests ($\alpha \leq 0.05$). Response: Height on caudex of species, Factor: Aspect of caudex individual occupies on caudex (4 classes, 1 = North, 2 = East, 3 = South, 4 = West); Response: Species frequency on caudex, Factor: Aspect of caudex individual occupies on caudex (4 classes, 1 = North, 2 = East, 3 = South, 4 = West); Response: Species frequency on caudex, Factor: Texture of caudex surface (up to 4 classes, 1 = rough, 2 = irregular, 3 = frizzy, 4 = debris ring). The number in brackets indicates which class has the greater average rank of the two. (***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$; ns, not significant; na, not applicable). Notation 1: Individual Kruskal-Wallis tests between classes conducted when applicable to determine which classes are significantly different; Notation 2: *Hymenophyllum rarum* with > 25 % sub-caudex foliage cover only occurred on sections of a caudex with a rough texture.

Species	Response	Factor	Combined classes	Individual classes ¹					
			H	1 v 2	1 v 3	1 v 4	2 v 3	2 v 4	3 v 4
<i>Hymenophyllum rarum</i>	Height on Caudex	Aspect	5.54 ns	ns	ns	ns	ns	ns	ns
<i>Microsorium pustulatum</i>	Height on Caudex	Aspect	1.85 ns	ns	ns	ns	ns	ns	ns
<i>Asplenium bulbiferum</i>	Frequency	Aspect	3.29 ns	ns	ns	ns	ns	ns	ns
<i>Crepidomanes venosum</i>	Frequency	Aspect	23.36 ***	2 **	3 ***	ns	ns	2 **	3 ***
<i>Grammitis billardierei</i>	Frequency	Aspect	2.87 ns	ns	ns	ns	ns	ns	ns
<i>Hymenophyllum flabellatum</i>	Frequency	Aspect	8.06 *	ns	3 ***	ns	ns	ns	ns
<i>Hymenophyllum rarum</i>	Frequency	Aspect	9.30 **	2 **	3 **	ns	ns	2 *	ns
<i>Microsorium pustulatum</i>	Frequency	Aspect	1.00 ns	ns	ns	ns	ns	ns	ns
<i>Rumohra adiantiformis</i>	Frequency	Aspect	2.24 ns	ns	ns	ns	ns	ns	ns
<i>Tmesipteris obliqua</i>	Frequency	Aspect	4.17 ns	ns	ns	ns	ns	ns	ns
<i>Asplenium bulbiferum</i>	Frequency	Texture	394.04 ***	1 ***	1 ***	1 ***	2 ***	2 ***	ns
<i>Crepidomanes venosum</i>	Frequency	Texture	285.99 ***	1 ***	1 ***	na	2 ***	na	na
<i>Grammitis billardierei</i>	Frequency	Texture	340.51 ***	1 ***	1 ***	na	ns	na	na
<i>Hymenophyllum flabellatum</i>	Frequency	Texture	90.08 ***	1 ***	1 ***	na	ns	na	na
<i>Hymenophyllum rarum</i>	Frequency	Texture	na ²	na	na	na	na	na	na
<i>Microsorium pustulatum</i>	Frequency	Texture	30.74 ***	ns	3 ***	ns	2 ***	ns	3 ***
<i>Rumohra adiantiformis</i>	Frequency	Texture	36.96 ***	ns	3 ***	ns	2 ***	ns	3 ***
<i>Tmesipteris obliqua</i>	Frequency	Texture	1.10 ns	ns	ns	na	ns	na	na



Figure 5.2 *Tmesipteris obliqua* growing on a *D. antarctica* caudex.

A significant variation was identified between the heights on *D. antarctica* caudices of mature (Class 2) and immature (Class 1) *Asplenium bulbiferum*, with mature individuals occurring at a greater height on average (Table 5.5). No significant variation was identified between the height of mature and immature *Grammitis billardiarei* on *D. antarctica* caudices (Table 5.5).

Discussion

The obligate vascular epiphytes of the *D. antarctica* caudex are overwhelmingly dominated by pteridophytes (ferns) (Table 5.1). In all, 11 epiphytic fern species were identified to have colonised the caudex of *D. antarctica* (Table 5.1) across the 19 sample plots of the study area. The only non-fern epiphyte species identified during the study was *Sarcochilus australis*, an orchid, which had colonised the outer branchlets of the woody shrub *Coprosma quadrifida* in two separate sites. The fern dominance of the epiphytic niche of lower shaded forest stratum is common globally (Kelly 1985, Parra *et al.* 2009, Zotz and Büche 2000). However, the Tasmanian vascular epiphyte flora is exceptionally depauperate

by global standards, especially considering the island's topographic, environmental and floristic diversity. In this respect, temperate latitudes are considered relatively depauperate compared with the high diversity of the tropics (Huston 1994, Schulze *et al.* 2005, Zotz 2005). For instance Kelly (1985) identified 69 “habitual epiphytes” (34 Angiosperms and 35 Pteridophytes) in a Jamaican forest. Other examples are the 1173 species identified in the forests of the Mexican State of Chiapas (Wolf and Alejandro 2003), a single tree hosted 85 species in the northern Bolivian Andes (Kromer *et al.* 2005) and a 75 ha patch of rainforest on New Zealand North Island contained 20 species (Burns and Dawson 2005).

Hygrophytic and shade adapted species, such as those of the family Hymenophyllaceae (filmy ferns), tend to dominate the lower trunk epiphytic niche in many wet forests globally (Kelly 1985, Parra *et al.* 2009, Zotz and Büche 2000). The study area was no exception with 6 species of filmy fern identified including *Crepidomanes venosum*, *Hymenophyllum flabellatum* and *Hymenophyllum rarum* (Table 5.1 and Figure 5.3). In addition to the filmy ferns, *Asplenium bulbiferum* and *Grammitis billardiarei* (Figure 5.4) also occurred predominantly on the lower section of the caudex, specifically that with a rough texture (Table 5.5). The moisture retention properties of the thick root mantle of the lower caudex (Ashton 1986, Roberts *et al.* 2005) (which is a common feature of several tree fern species (Mehltreter *et al.* 2005)) provide a substrate suitable for colonisation by hygrophytic filmy ferns. In this study, importance of a mesic environment to the lower caudex epiphytes is highlighted by their lower frequencies and lower diversity with increasing maximum temperature of the forest site (Appendix 2, Table 2.1), hence increasing evaporative demand during drier conditions. However, the respective frequencies of epiphyte species show no variation with changing rainfall or canopy closure (except *Hymenophyllum rarum*) even though these factors can also influence moisture availability (Appendix 2, Table 2.1).

The caudex apex is more exposed and insolated compared to the mesic conditions of the lower caudex. Consequently, epiphytes at the apex will need to endure a relatively xeric microclimate at least seasonally if not diurnally. However, the potential for the apex to dry



Figure 5.3 Dominance of lower *D. antarctica* caudices by species of filmy ferns.



Figure 5.4 *Asplenium bulbiferum* (arrow) and *Grammitis billardierei* (arrow) growing on the caudex of *D. antarctica*.

out is probably reduced by the typically shaded environment which large *D. antarctica* occupy and the propensity of its fronds to funnel water and litter (which acts as a protective mulch) to the apex of the fern. The *D. antarctica* fronds will also protect apical epiphytes

from the evaporative effect of wind. Therefore epiphytes of the *D. antarctica* apex do not need to be xerophytes, but must still be able to minimise moisture loss to survive periods of moisture deficit.

Only two epiphytes *Microsorium pustulatum* (Polypodiaceae) and *Rumohra adiantiformis* (Dryopteridaceae) (Table 5.1) occurred at the apex of the caudex and were typically situated just above, just below and around the frond bases (Figure 5.5). These two species occurred in dense colonies at the top of medium and large *D. antarctica*, suggesting their intolerance of the combined shading by the canopy strata and their host's fronds that would typically occur lower on the caudex. The ability of *Microsorium pustulatum* and *Rumohra adiantiformis* to survive varying moisture regimes is evident in the lack of a response in their frequency to variations in mean maximum temperature, mean annual rainfall and canopy closure (Appendix 2 Table 2.1). It is likely *Microsorium pustulatum* and *Rumohra adiantiformis* have evolved to possess a moisture use strategy that enables the successful colonisation of drier and more insulated substrates. Other epiphytic species of the families Polypodiaceae and Dryopteridaceae (not present in Tasmania) have been identified to possess conservative water use strategies that enable them to survive microclimates of varying dryness (Dubuisson *et al.* 2009).

The importance of medium and large sized *D. antarctica* to vascular epiphyte diversity is evident in the strong positive correlation between species richness and *D. antarctica* erect caudex length (Table 5.4). Although the epiphyte diversity on other host species, e.g. trees and shrubs was not sampled in this study, field observations revealed lower tree trunks that were frequently bare of vascular epiphytes, or an epiphyte diversity that rarely rivalled that of *D. antarctica*. The upper tree canopy also supported vascular epiphytes, with *Microsorium pustulatum* being particularly conspicuous (Figure 5.6). However, the inaccessibility of the tree canopy prevented closer observation of the arboreal epiphyte flora.



Figure 5.5 *Rumohra adiantiformis* (arrow) that has colonised the apex of a *D. antarctica* caudex.

The positive correlation between erect caudex length and the frequencies of respective epiphyte species (except for *Tmesipteris obliqua*) as well as species richness (Table 5.4) can be explained by the greater surface available for colonisation of the caudex of larger *D. antarctica*. This is also a likely explanation for the correlation between rough caudex length and the frequency of *Crepidomanes venosum*, *Grammitis billardierei* and *Hymenophyllum flabellatum* (Table 5.4), species which were found predominantly on the rough textured surface (class 1). The non-significant and minor correlations between species frequencies and the irregular and frizzy caudex surface textures (Table 5.4) highlight the importance of the rough textured lower caudex to the majority of epiphytes. Although *Microsorium pustulatum* and *Rumohra adiantiformis* occur predominantly on the frizzy textured surface they do so largely at or near the caudex apex. Hence a longer section of frizzy textured caudex will not necessarily lead to greater frequencies of *Microsorium pustulatum* and *Rumohra adiantiformis* (Table 5.4). Frond size, live frond frequency and residual

(marcescent) frond frequency also appear not to influence the frequency of *Microsorium pustulatum* and *Rumohra adiantiformis* and vice versa (Table 5.4).

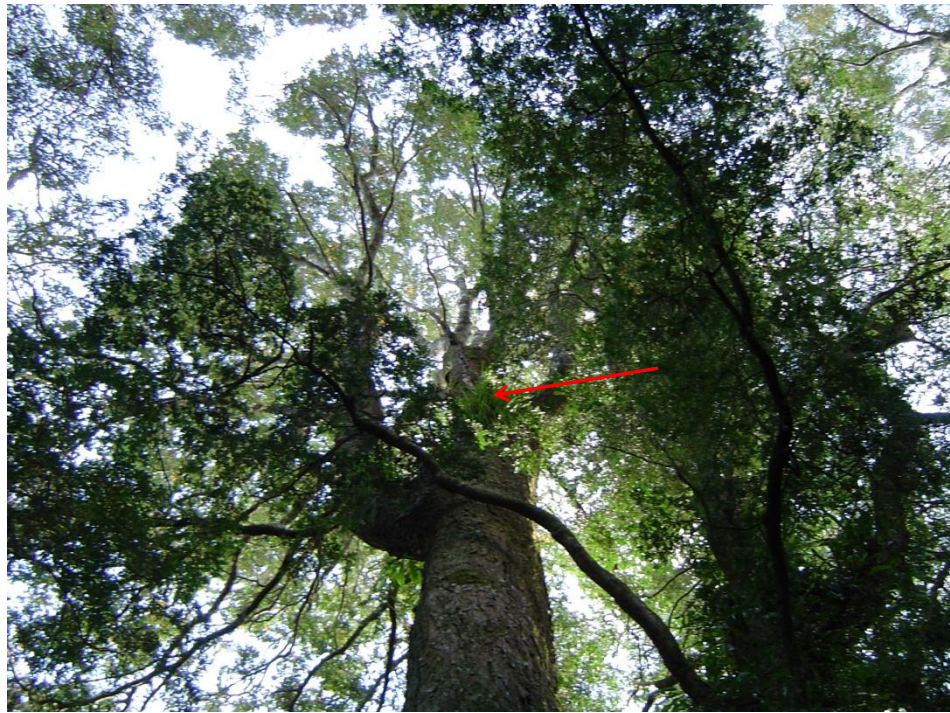


Figure 5.6 *Microsorium pustulatum* (arrow) that has colonised the trunk of a *Nothofagus cunninghamii*.

This is an interesting result since it could be expected that either of the apical epiphytes (*Microsorium pustulatum* and *Rumohra adiantiformis*) would smother or damage emerging croziers or the tree fern's fronds would shade out the apical epiphytes. However, neither of these two scenarios appears to occur. Perhaps the growth rate of the apical epiphytes is slow enough to enable the flush of emerging tree fern fronds to push away epiphyte rhizomes (out and down) from the rosette centre thereby protecting subsequent crozier emergences. In such a case sufficient light is evidently still accessible to the apical epiphytes either by positioning their fronds between and above the frond bases or by accessing light that shines through the gap between adjacent frond stipes. Furthermore the potential disadvantages of apical epiphytes to *D. antarctica* may be outweighed by their occupation of a niche that could be filled otherwise by more damaging climbers. Although climbers were not observed to dominate *D. antarctica* caudices in any of the field sites,

other tree fern species have been reported to be severely damaged by climber infestations (Page and Brownsey 1986).

The negative correlation of epiphyte frequency on the lower caudex and debris ring length (Table 5.4) may be due to shading or smothering of these epiphytes by fine debris that erodes from the base and sides of the ring. Another explanation is that the debris ring may retain moisture and limit the volume of stemflow down the caudex, reducing moisture availability for the sensitive filmy ferns. Apical epiphytes possess a similar negative correlation with debris ring length, but they grow at the level and on top of the debris ring. Litter accumulating at the centre of the apical frond rosette may be smothering the apical epiphytes. Alternatively the fronds of apical epiphytes growing on the sides of the debris ring could be positioned closer to the wider section of the tree fern's lamina and hence under greater shade.

Other than for *Asplenium bulbiferum* and *Crepidomanes venosum*, the frequency of epiphyte species on *D. antarctica* caudices showed no relationship with frond size or frond frequency (Table 5.4). It is possible that a dense frond layer at the apex of the caudex will by itself not sufficiently shade the lower caudex to exclude the filmy fern species as these are typically shade adapted (Proctor 2003). Frequencies of *Asplenium bulbiferum* showed a positive correlation with frond frequency and frond area index and *Crepidomanes venosum* a positive correlation with frond frequency and lamina maximum width (Table 5.4) perhaps indicating its intolerance of direct insolation.

The greater height of *Grammitis billardiarei* occurring on the northern and western aspects of the caudex is unusual (Appendix 2, Table 2.1). Epiphytes occurring on these aspects could be expected to be exposed to drier conditions, i.e. north has greater insolation especially during the afternoon and the north-west surface is exposed to the prevailing winds when VPD is maximised diurnally. Even if *Grammitis billardiarei* is adapted to these conditions it is unusual that it occurs lower on the caudex on the relatively shaded and

protected southern and eastern aspects. Perhaps residual fronds on the northern and western aspects are dislodged more often by wind than those of the southern and eastern aspects, which prevents the establishment of *Grammitis billardiarei* higher on the caudex, but why not for other epiphytes?

The greater frequency of the filmy fern species *Crepidomanes venosum* on the eastern and southern aspects of the caudex is most likely due to dependence on a hydric microclimate (Table 5.5). The two other filmy ferns *Hymenophyllum flabellatum* and *Hymenophyllum rarum* also showed a similar, but not as pronounced tendency towards higher frequencies on the southern and/or eastern aspects of the caudex (Table 5.5).

Mature *Asplenium bulbiferum* specimens occur higher on the caudex than smaller immature individuals (Table 5.5). A possible explanation for the difference is browsing of *Asplenium bulbiferum* by wallabies (Neyland 1991). Browsing animals can be expected to select against *Asplenium bulbiferum* from ground level to a height within their reach. Consequently juvenile *Asplenium bulbiferum* within the reach of browsers have a greater chance of removal, which will skew the cumulative population distribution of mature individuals toward a greater height on the caudex.

Conclusion

Eleven species of obligate epiphyte were identified on the caudex of *D. antarctica*. Eight of these species possessed sufficient frequency and distribution across the field sites to provide a sound statistical basis to this investigation.

The investigation identified two main epiphyte colonisation zones on the *D. antarctica* caudex, which are largely delineated by microclimate and substrate conditions. The first zone consists of the lower caudex, which is composed of a thick fibrous rough textured root mantle. The high moisture retentiveness of the root mantle and greater humidity of the lower understorey enabled this zone to be dominated by hygrophytic vascular epiphytes,

such as those of the family Hymenophyllaceae, particularly *Crepidomanes venosum*. The filmy ferns generally occur at a greater frequency on the sheltered and shaded eastern and southern aspects of the caudex which feature the most mesic microsite conditions available. Dependence of the lower caudex epiphytes on a moist microclimate is evidenced by their reduced frequency as maximum temperature and therefore evapotranspiration increases across the sample sites.

The second epiphyte colonisation zone is the caudex apex. This zone is colonised by epiphytes that can survive a drier more exposed microclimate compared to the lower caudex. Only two rhizomatous epiphytes, *Microsorium pustulatum* and *Rumohra adiantiformis*, colonise the caudex apex. Both species, like some of their relatives, most likely possess a conservative water use strategy, which enables them to access the greater insolation of exposed substrates, such as the caudex apex. Neither species appears to tangle the crown of *D. antarctica* and if they help prevent the establishment of more damaging climbers then the apical epiphytes could be in a form of mutualistic relationship with *D. antarctica*.

In between the lower caudex and caudex apex zones is typically a length of caudex largely devoid of obligate epiphytes. The surface of this intermediate section consists of protruding stipe bases between which is a tangle of basal frond hairs and litter. This section of caudex is probably shaded enough to prevent colonisation by the apical epiphytes but too dry to enable the survival of the lower caudex epiphytes.

Chapter 6: The regeneration of typically terrestrial plant species on the caudex of *Dicksonia antarctica*

Introduction

The extent to which facultative epiphytes occur epiphytically or terrestrially varies among and within species (Moffett 2000). Many facultative epiphytes are typically terrestrial species that lack specific adaptations for life as an epiphyte and are generally dependent upon organic matter accumulations, particularly suspended soil and decomposing humus, to provide nutrition, moisture, and anchorage in the canopy (Benzing 2008, Enloe *et al.* 2006, Mucunguzi 2007, Sillett and Bailey 2003, Sillett and Van Pelt 2007). It can take a long time for a woody host (e.g. a tree) to develop the architecture and structure that will entrain sufficient organic matter to enable the successful establishment of facultative epiphytes. In *Sequoia sempervirens* Endl. (Coastal Redwood), for example, branches and crotches need to be large and stable before litter will sufficiently accumulate, and this can take centuries (Enloe *et al.* 2006). Even then facultative epiphytes hosted by trees tend to be limited to relatively smaller species (herbs and shrubs) or dwarf individuals of larger species (Preston 2007).

In contrast to trees, several species of tree fern provide a substrate suitable for the establishment and regeneration of terrestrial plant species. These species of tree fern develop a fibrous root mantle around the lower portion of their erect caudex, which forms a continuum with the soil. Stemflow and decomposition of entrapped litter (within the crown and root mantle) and the root mantle substrate typically provide enough nutrition for shrubs or trees to grow slowly after germinating on the tree fern's root mantle or within the basket of litter which is concentrated in the apical rosette of the fern (Dearden and Wardle 2008, Gaxiola *et al.* 2008). Sufficient nutrition to reach maturity is attained when the epiphyte's root system reaches the soil via the root mantle-soil continuum. If they can survive epiphytically on a tree fern's root mantle, most species of larger trees and shrubs will

eventually root in the ground, which strictly speaking defines them as facultative primary hemi-epiphytes (Moffett 2000). However, depending on their proximity to the ground, smaller species of primarily terrestrial shrubs, herbs or ferns that can survive and regenerate epiphytically on a tree fern's root mantle may never root in the ground, due to their typically smaller root system. This defines them as facultative epiphytes. In either case the colonising species' habits are facultative with respect to the tree fern. Hence for this purpose they will be referred to as facultative epiphytes regardless of whether or not they eventually root in the ground after germinating on a *D. antarctica* caudex.

The consequence of tree ferns being a dominant or co-dominant regeneration substrate for co-occurring shrub and tree species can render them more or less essential for maintaining the population density of those species. One example involves the New Zealand tree ferns *D. squarrosa* and *Cyathea smithii*, which facilitate the regeneration of a range of species, such as *Griselinia littoralis* Raoul, *Myrsine australis* and *Weinmannia racemosa* (Gaxiola *et al.* 2008, Veblen and Stewart 1980). The continuing importance of *D. squarrosa* and *Cyathea smithii* to co-occurring species is due to their provision of a regeneration substrate above the browse layer of introduced deer (Gaxiola *et al.* 2008) and/or a substrate largely free of litter that can smother seedlings. Another example occurs in the montane ridge forests of Jamaica's Blue Mountains, where the tree fern *Cyathea pubescens* is the main site for *Clethra occidentalis* regeneration (Newton and Healey 1989). In south-eastern Australia several woody plant species in moist forest e.g. *Acacia melanoxylon*, *Atherosperma moschatum*, *Coprosma quadrifida*, *Nothofagus cunninghamii*, *Olearia argophylla*, *Phyllocladus aspleniifolius*, *Pittosporum bicolor* Hook. and *Tasmania lanceolata* (Poir.) A.C.Sm. have been observed to establish on the root mantle of the tree fern *D. antarctica* (Ashton 2000, Garrett 1996b, Ough and Ross 1992).

In the Australian context, other than the above and like observations, specific research into the regeneration of terrestrial species on tree ferns is deficient. *Dicksonia antarctica* is an excellent research species for this purpose, for it readily develops a thick root mantle, is a

common component of many south-eastern Australian wet forests, and terrestrial species have been observed to reach maturity after germinating on it. Building on these observations quantitatively this chapter will test the hypotheses that:

- Seedlings (< 0.20 m tall), established plants (≥ 0.20 m to < 3 m tall) and mature plants (≥ 3 m tall) occur with greater frequency on *D. antarctica* caudices compared to each of the other available substrates, i.e. on fallen *D. antarctica* caudices (FC), on coarse woody debris (CWD), on soil and litter (Soil), and as coppice (Copp). The production of coppice is a regeneration strategy employed by some species and is included as a substrate class so its frequencies can be compared with those of plants that had germinated on the substrate types outlined above; and
- The height distribution of facultative epiphytes on *D. antarctica* caudices differs between seedlings (< 0.20 m tall) and established/mature plants (≥ 0.20 m tall) of the same species; and
- The height distribution of established (≥ 0.20 m to < 3 m tall) and mature plants (≥ 3 m tall) on *D. antarctica* caudices differs between facultative epiphyte species.

The reasoning behind these hypotheses is that *D. antarctica* caudices may serve as a refuge from disturbances occurring on the forest floor and these can lead to the death of colonising seedlings. For instance *Atherosperma moschatum* and *Pittosporum bicolor*, which co-occur with *D. antarctica*, are particularly favoured by native browsers (Hickey *et al.* 1982, McLeod and Gray 2005, Neyland 1991) and both have been observed growing on *D. antarctica* caudices (Ough and Ross 1992) in Tasmania.

The distribution of facultative epiphytes on the *D. antarctica* caudex will be influenced by the microclimate and substrate conditions present as these will impact germination success and seedling survival. These factors are in turn likely to be influenced by the tree fern's architecture. For example the size and number of fronds will influence the amount of sunlight reaching the facultative epiphytes, whereas the root mantle thickness will influence the amount of root space available for facultative epiphytes as well as the reservoir of

moisture and nutrients available to them. Based on this argument the current chapter will test the hypotheses that:

- The frequencies of facultative epiphyte seedlings (< 0.20 m tall) and established/mature plants (≥ 0.20 m tall) are positively associated with the rough surface texture of the *D. antarctica* caudex. The germination and establishment success should be greater here as the thick moisture retentive root mantle that forms the rough surface texture is likely to be conducive to the requirements of the main facultative epiphyte species;
- The frequencies of facultative epiphyte seedlings (< 0.20 m tall) and established/mature plants (≥ 0.20 m tall) are positively associated with those parts of the *D. antarctica* caudex facing either a southern or eastern aspect as these provide a more sheltered microclimate for germination and growth;
- The frequencies of seedling (< 0.20 m tall) and established (≥ 0.20 m to < 3 m tall) facultative epiphyte species on each of the four substrates (i.e. upright *D. antarctica* caudices, fallen *D. antarctica* caudices (FC), coarse woody debris (CWD) and soil and litter (Soil)) are negatively correlated with foliage projective cover (FPC) of the forest canopy. Increasing foliage projective cover will correspond with less sunlight reaching the lower understorey which may lessen establishment success;
- The frequencies of facultative epiphyte seedlings (< 0.20 m tall) and established/mature plants (≥ 0.20 m tall) are positively associated with *D. antarctica* caudices ≥ 3 m long, as ferns this size are likely to be the oldest and possess the larger area of rough textured and thick caudex in which facultative epiphytes can germinate and establish;
- The frequencies of seedling (< 0.20 m tall) and established/mature (≥ 0.20 m tall) facultative epiphyte species on *D. antarctica* caudices are positively correlated with *D. antarctica* maximum diameter, caudex length and caudex length with a rough textured surface;
- The frequencies of seedling (< 0.20 m tall) and established/mature (≥ 0.20 m tall) facultative epiphyte species on *D. antarctica* caudices are negatively correlated with *D. antarctica* frond size, frequency, residual frond frequency, and crown area index (CAI). Fronds will shade facultative epiphytes thereby limiting sunlight, a resource essential to

their survival, whereas residual (marcescent) fronds can smother facultative epiphytes; and

- Seedlings (< 0.20 m tall), established plants (≥ 0.20 m to < 3 m tall) and mature plants (≥ 3 m tall) occur with greater frequencies on forest sites classed as being of high fertility compared to those of low fertility.

Only those terrestrial plant species which were sufficiently represented across the field sites in north-eastern Tasmania were included in this investigation, namely *Atherosperma moschatum*, *Coprosma quadrifida*, *D. antarctica*, *Nothofagus cunninghamii*, *Olearia argophylla*, *Pittosporum bicolor* and *Tasmannia lanceolata* (selection criteria outlined in Chapter 3).

Analysis

The 19 field sample plots described in Chapter 3 (Site Selection and Field Sampling) provided the database for this analysis of morphological, epiphytic and site variables associated with *D. antarctica* in north-east Tasmania. A glossary of abbreviations appears on page 9 of this thesis.

The Kruskal-Wallis Test ($\alpha 0.05$) (MINITAB 2005) was used to test the hypothesis that:

- Seedlings (< 0.20 m tall), established plants (≥ 0.20 m to < 3 m tall) and mature plants (≥ 3 m tall) occur with greater frequency on *D. antarctica* caudices compared to each of the other available substrates, i.e. on fallen *D. antarctica* caudices (FC), on coarse woody debris (CWD), on soil and litter (Soil), and as coppice (Copp).

In this test frequency is the response variable and substrate class is the factor. Coppice is only applicable as a substrate class for those species that produced coppice within the field sites. Separate Kruskal-Wallis Tests were conducted for each species' seedlings, established plants and mature plants respectively, i.e. the frequencies of different species were not combined and neither were the frequencies of seedlings, established plants or

mature plants. If significant variation was identified among the substrate classes, further Kruskal-Wallis Tests were conducted on the frequencies of each pair of classes to identify between which classes significant variation occurred, for example, the frequency of < 0.20 m tall *Pittosporum bicolor* on coarse woody debris (CWD) versus the frequency of < 0.20 m tall *Pittosporum bicolor* on *D. antarctica* caudices (DaC). If identified as significantly different, the substrate class with the greater median is that with the greatest frequency. If a substrate supports a significantly greater frequency of seedlings (< 0.20 m tall) of a species compared to the other possible substrates it highlights that substrate as the likely dominant germination substrate for that species. Furthermore if a substrate supports a significantly greater frequency of established (\geq 0.20 m to < 3 m tall) individuals of a species compared to other possible substrates it highlights that substrate as the likely dominant establishment substrate for that species.

The Kruskal-Wallis Test (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- The frequencies of facultative epiphyte seedlings (< 0.20 m tall) and established/mature plants (\geq 0.20 m tall) are positively associated with the rough surface texture of the *D. antarctica* caudex.

In this test frequency is the response variable and caudex surface texture class is the factor. Separate Kruskal-Wallis Tests were conducted for each species' seedlings and established/mature plants, i.e. the frequencies of different species were not combined and neither were the frequencies of seedlings or established/mature plants. If significant variation was identified among the caudex surface texture classes, further Kruskal-Wallis Tests were conducted on the frequency of each pair of classes to identify between which classes significant variation occurred, for example, the frequency of < 0.20 m tall *Pittosporum bicolor* on rough textured caudex versus the frequency of < 0.20 m tall *Pittosporum bicolor* on irregular textured caudex. If identified to be significantly different, the caudex surface texture class with the greater median is that with the greatest frequency.

The Kruskal-Wallis Test (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- The frequencies of facultative epiphyte seedlings (< 0.20 m tall) and established/mature plants (≥ 0.20 m tall) are positively associated with those parts of the *D. antarctica* caudex facing either a southern or eastern aspect.

In this test frequency is the response variable and caudex aspect class is the factor. Separate Kruskal-Wallis Tests were conducted for each species' seedlings and established/mature plants, i.e. the frequencies of different species were not combined and neither were the frequencies of seedlings or established/mature plants. If significant variation was identified among the caudex aspect classes, further Kruskal-Wallis Tests were conducted on the frequencies of each pair of classes to identify between which classes significant variation occurred, for example, the frequency of < 0.20 m tall *Pittosporum bicolor* on the southern facing caudex versus the frequency of < 0.20 m tall *Pittosporum bicolor* on the northern facing caudex. If identified to be significantly different, the caudex aspect class with the greater median is that with the greatest frequency. Testing of this hypothesis helps to reveal if caudex aspect influences the germination and establishment of facultative epiphytes.

The Kruskal-Wallis Test ($\alpha 0.05$) (MINITAB 2005) was used to test the hypothesis that:

- Seedlings (< 0.20 m tall), established plants (≥ 0.20 m to < 3 m tall) and mature plants (≥ 3 m tall) occur with greater frequency on sites classed as being of high fertility compared to those classes as being of low fertility.

In this test frequency is the response variable and site fertility class is the factor. Separate Kruskal-Wallis Tests were conducted for each species' seedlings, established and mature plants, i.e. the frequency of different species were not combined and neither were the frequencies of seedlings, established or mature plants.

The Kruskal-Wallis Test ($\alpha 0.05$) (MINITAB 2005) was used to test the hypothesis that:

- The height distribution on *D. antarctica* caudices of facultative epiphytes differs between seedlings (< 0.20 m tall) and established/mature plants (≥ 0.20 m tall) of the same species.

In this test, attachment height is the response variable and growth stage (seedling or established/mature) is the factor. Separate Kruskal-Wallis Tests were conducted for each species.

The Kruskal-Wallis Test (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- The height distribution on *D. antarctica* caudices of established (≥ 0.20 m to < 3 m tall) and mature plants (≥ 3 m tall) differ between facultative epiphyte species.

In this test, attachment height is the response variable and facultative epiphyte species (established or mature) is the factor. Separate Kruskal-Wallis Tests were conducted for each growth stage (established or mature) between each pair of species. Similarities between each species' establishment heights on *D. antarctica* caudices can help to reveal whether they are undergoing similar establishment restrictions.

The Kruskal-Wallis Test (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- The frequencies of facultative epiphyte seedlings (< 0.20 m tall) and established/mature plants (≥ 0.20 m tall) are positively associated with *D. antarctica* caudices ≥ 3 m long.

In this test, frequency is the response variable and caudex size class (< 2 m long, ≥ 2 to < 3 m long and ≥ 3 m long) is the factor. Separate Kruskal-Wallis Tests were conducted for each species' seedlings and established/mature plants, i.e. the frequencies of different species were not combined and neither were the frequencies of seedlings or established/mature plants. If significant variation was identified among the caudex size classes, further Kruskal-Wallis Tests were conducted on the frequency of each pair of classes to identify between which classes significant variation occurred, for example, the frequency of < 0.20 m tall *Pittosporum bicolor* on caudex size class < 2 m long versus the frequency of < 0.20 m tall *Pittosporum bicolor* on caudex size class ≥ 3 m long. If identified to be significantly different, the caudex size class with the greater median is that with the greatest frequency.

The Spearman's rank correlation (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- The frequencies of seedling (< 0.20 m tall) and established (≥ 0.20 m to < 3 m tall) facultative epiphyte species on each and a combination of the four substrates (i.e. upright *D. antarctica* caudices, fallen *D. antarctica* caudices (FC), coarse woody debris (CWD) and soil and litter (Soil)) are negatively correlated with foliage projective cover (FPC) of the forest strata.

The mid-range values of foliage projective cover (FPC) the separate and combined canopy strata (outlined in Chapter 3) were used respectively.

The Spearman's rank correlation (α 0.05) (MINITAB 2005) was used to test the hypotheses that:

- The frequencies of seedling (< 0.20 m tall) and established/mature (≥ 0.20 m tall) facultative epiphyte species on *D. antarctica* caudices are negatively correlated with *D. antarctica* frond size, frequency, residual frond frequency, and crown area index (CAI); and
- The frequencies of seedling (< 0.20 m tall) and established/mature (≥ 0.20 m tall) facultative epiphyte species on *D. antarctica* caudices are positively correlated with *D. antarctica* maximum diameter, caudex length and caudex length with a rough textured surface.

The test was conducted on each facultative epiphyte species in each of the three size classes (< 0.20 m tall, ≥ 0.20 m tall and combined).

Results

Thirty-two typically terrestrial plant species were identified as either rooted epiphytically or hemi-epiphytically in *D. antarctica* caudices across the field sites (Table 6.1). Twenty-two of these species were represented in part by mature or near mature individuals and 10 others by established juveniles only (not just germinates) on *D. antarctica* host plants (Table 6.1). Germinates of *Acacia* spp. were present epiphytically on *D. antarctica*, at several sites, but

were only identifiable to the generic level (Table 6.1). Six species were identified to possess sufficient frequency and distribution as facultative epiphytes (according to criteria outlined in Chapter 3) to be included in the data analysis. These were *Atherosperma moschatum*, *Coprosma quadrifida*, *Nothofagus cunninghamii*, *Olearia argophylla*, *Pittosporum bicolor*, and *Tasmannia lanceolata* (Table 6.1).

All four substrates (*D. antarctica* caudices (DaC), fallen *D. antarctica* caudices (FC), coarse woody debris (CWD) and soil and litter (soil)) supported a similar frequency of *Atherosperma moschatum* seedlings (< 0.20 m tall) (Appendix 3, Table 3.1). The combined frequency of *Atherosperma moschatum* seedlings on elevated substrates (DaC, FC and CWD) was greater than that for soil (Appendix 3, Table 3.1). *Dicksonia antarctica* caudices supported the greatest frequency of established (≥ 0.20 to < 3 m tall) *Atherosperma moschatum* out of all available substrates, but it was not different from the frequency of comparatively sized *Atherosperma moschatum* as coppice (≥ 0.20 to < 3 m tall) (Appendix 3, Table 3.1). Frequency of established (≥ 0.20 to < 3 m tall) *Atherosperma moschatum* as coppice was greater than the frequency of established *Atherosperma moschatum* supported by each of the substrates FC, CWD and Soil, but it was not different from the combined frequency of established *Atherosperma moschatum* supported by elevated substrates (DaC, FC and CWD) (Appendix 3, Table 3.1).

Soil was the dominant substrate for mature (≥ 3 m tall) *Atherosperma moschatum*, but it did not support a frequency of mature *Atherosperma moschatum* that differed from the frequency of comparatively sized (≥ 3 m tall) *Atherosperma moschatum* coppice (Appendix 3, Table 3.1). Use of elevated substrates exceeded soil as a medium for germination of *Atherosperma moschatum*, with *Atherosperma moschatum* on erect *D. antarctica* caudices and *Atherosperma moschatum* as coppice composing the majority of established (≥ 0.20 to < 3 m tall) *Atherosperma moschatum* (Appendix 3, Table 3.1 and). The majority of the mature (≥ 3 m tall) and presumably the oldest *Atherosperma moschatum* appear to have originally germinated on soil or arisen from coppice (Appendix 3, Table 3.1).

Table 6.1 Plant species identified as growing epiphytically on *D. antarctica* caudices. Facultative epiphytes are labelled (f) and secondary hemi-epiphytes are labelled (h). The ‘common facultative epiphyte’ species are marked (*). Facultative epiphyte species represented by juveniles are marked (j). Introduced species are marked (#). *Acacia* spp. marked (●) are unable to be identified to the species level, potentially either *Acacia dealbata*, *Acacia mearnsii* or *Acacia melanoxylon*. (NA, not applicable). Note 1: Mean plant height in the case of angiosperms and gymnosperms is stem length. In the case of *D. antarctica* it is the erect caudex length, for remaining pteridophytes it is the length of the longest frond.

Species	Family	< 0.20 m tall					≥ 0.20 m tall				
		Frequency all sites	Height on Caudex (m)			Mean Plant Height (m) ¹	Frequency all sites	Height on Caudex (m)			Mean Plant Height (m) ¹
			Min	Mean	Max			Min	Mean	Max	
<i>Acacia melanoxylon</i> (f)	Mimosaceae	NA	NA	NA	NA	NA	5	0.44	0.75	1.40	12.00
<i>Acacia</i> spp. (j ●)	Mimosaceae	13	0.00	0.80	1.56	0.05	NA	NA	NA	NA	NA
<i>Aristotelia peduncularis</i> (f)	Elaeocarpaceae	8	1.48	2.64	2.99	0.10	11	1.32	2.57	3.16	0.62
<i>Atherosperma moschatum</i> (f*)	Atherospermataceae	50	0.00	0.88	3.4	0.03	72	0.08	1.69	4.53	6.00
<i>Blechnum watsii</i> (f)	Blechnaceae	27	0.00	0.56	2.05	0.07	36	0.00	0.65	2.30	0.47
<i>Clematis aristata</i> (f)	Ranunculaceae	1	0.49	0.49	0.49	0.04	1	1.16	1.16	1.16	0.60
<i>Coprosma nitida</i> (f)	Rubiaceae	NA	NA	NA	NA	NA	1	2.15	2.15	2.15	0.45
<i>Coprosma quadrifida</i> (f*)	Rubiaceae	61	0.00	0.38	1.81	0.04	18	0.07	1.23	2.87	0.75
<i>Dicksonia antarctica</i> (f)	Dicksoniaceae	33	0.00	1.41	4.57	0.00	16	0.110	1.35	2.73	0.11
<i>Gaultheria hispida</i> (j f)	Ericaceae	3	1.60	1.63	1.67	0.11	NA	NA	NA	NA	NA
<i>Histiopteris incisa</i> (h)	Dennstaedtiaceae	NA	NA	NA	NA	NA	4	0.00	0.68	1.35	NA
<i>Hydrocotyle hirta</i> (h)	Apiaceae	1	1.50	1.50	1.50	0.02	NA	NA	NA	NA	NA
<i>Hypolepis rugosula</i> (h)	Dennstaedtiaceae	1	0.30	0.30	0.30	0.18	4	0.05	0.25	0.45	0.33
<i>Lilaeopsis polyantha</i> (f)	Apiaceae	1	0.00	0.00	0.00	0.10	NA	NA	NA	NA	NA
<i>Monotoca</i> spp. (f)	Epacridaceae	1	1.10	1.10	1.10	0.02	4	0.63	1.10	1.68	6.00
<i>Muehlenbeckia gunnii</i> (f)	Polygonaceae	4	0.25	1.02	2.72	0.06	6	0.58	1.14	1.86	2.88
<i>Nothofagus cunninghamii</i> (f*)	Fagaceae	72	0.00	0.50	3.32	0.04	24	0.52	2.10	3.94	9.13
<i>Olearia argophylla</i> (f*)	Asteraceae	275	0.00	0.73	3.42	0.04	15	1.00	1.19	3.90	1.19
<i>Olearia lirata</i> (f)	Asteraceae	3	0.45	1.48	2.45	0.06	1	1.13	1.13	1.13	6.00
<i>Ozothamnus rosmarinifolius</i> (j f)	Asteraceae	5	0.06	0.19	0.48	0.04	NA	NA	NA	NA	NA
<i>Phyllocladus aspleniifolius</i> (j f)	Podocarpaceae	1	1.88	1.88	1.88	0.73	NA	NA	NA	NA	NA
<i>Pimelea drupacea</i> (j f)	Thymelaeaceae	1	1.14	1.14	1.14	0.02	NA	NA	NA	NA	NA
<i>Pittosporum bicolor</i> (f*)	Pittosporaceae	111	0.00	1.47	4.63	0.06	101	0.25	1.82	4.56	2.54

Table continued next page

Table 6.1 Continued

Species	Family	< 0.20 m tall					≥ 0.20 m tall				
		Frequency all sites	Height on Caudex (m)			Mean Plant Height (m) *	Frequency all sites	Height on Caudex (m)			Mean Plant Height (m) *
			Min	Mean	Max			Min	Mean	Max	
<i>Polystichum proliferum</i> (f)	Dryopteridaceae	75	0.00	0.66	1.98	0.07	48	0.00	0.75	2.70	0.45
<i>Pomaderris apetala</i> (j f)	Rhamnaceae	23	0.00	0.61	1.05	0.05	NA	NA	NA	NA	NA
<i>Prostanthera lasianthos</i> (f)	Lamiaceae	NA	NA	NA	NA	NA	3	2.33	2.71	2.95	3.13
<i>Pteridium esculentum</i> (h)	Dennstaedtiaceae	NA	NA	NA	NA	NA	1	0.00	0.00	0.00	0.80
<i>Pterostylis pedunculata</i> (f)	Orchidaceae	2	0.37	0.37	0.37	0.08	NA	NA	NA	NA	NA
<i>Pultenaea juniperina</i> (j f)	Fabaceae	1	1.81	1.81	1.81	0.04	NA	NA	NA	NA	NA
<i>Rubus fruticosus</i> (f #)	Rosaceae	1	2.14	2.14	2.14	0.05	2	0.80	1.30	1.80	0.89
<i>Senecio</i> spp. (f)	Asteraceae	2	0.75	0.78	0.80	0.06	NA	NA	NA	NA	NA
<i>Tasmannia lanceolata</i> (f*)	Winteraceae	55	0.07	1.34	3.52	0.06	52	0.14	1.89	3.80	1.38
<i>Zieria arborescens</i> (J f)	Rutaceae	4	0.20	0.42	1.43	0.05	NA	NA	NA	NA	NA

Soil supports the greatest frequency of *Coprosma quadrifida* seedlings (< 0.20 m tall), with no significant variation identified among the frequencies occurring on the other substrates (Appendix 3, Table 3.1). Soil appears to be the current dominant germination medium of *Coprosma quadrifida*, although germination also occurs on the other substrates. Soil and erect *D. antarctica* caudices (DaC) support similar frequencies of established (≥ 0.20 to < 3 m tall) *Coprosma quadrifida* indicating the importance of both substrates to the persistence of the species in the moist forest understorey. Large (≥ 3 m tall) *Coprosma quadrifida* were observed to be a host for the epiphytic orchid *Sarcochilus australis*.

None of the four substrates (DaC, FC, CWD and soil) supported a singularly dominant frequency of *Nothofagus cunninghamii* seedlings (< 0.20 m tall), although the frequency of *Nothofagus cunninghamii* seedlings supported by coarse woody debris (CWD) was greater than that supported by DaC and fallen *D. antarctica* caudices (FC), but not greater than in Soil. Each of the substrates (DaC, FC, CWD and soil) supported similar frequencies of established (≥ 0.2 to < 3 m tall) *Nothofagus cunninghamii*. The frequency of mature (≥ 3 m) *Nothofagus cunninghamii* supported by soil was greater than the frequency of mature *Nothofagus cunninghamii* coppice and the frequency of mature *Nothofagus cunninghamii* supported by the remaining substrates. The frequency of mature *Nothofagus cunninghamii* coppice was greater than the frequency of mature *Nothofagus cunninghamii* supported by either FC or CWD, but not that supported by erect *D. antarctica* caudices (DaC) (Appendix 3, Table 3.1).

Dicksonia antarctica caudices (DaC) supported a greater frequency of *Olearia argophylla* seedlings (< 0.20 m tall) than either FC or CWD. Both DaC and Soil supported similar frequencies of *Olearia argophylla* seedlings, but the frequency of seedlings on soil was not different to the frequency of *Olearia argophylla* seedlings supported by FC. Established (≥ 0.2 to < 3 m tall) and mature (≥ 3 m) *Olearia argophylla* were only supported by either soil or DaC (). The frequency of established *Olearia argophylla* supported by either soil or DaC

was similar, whereas the frequency of mature *Olearia argophylla* was different between Soil and DaC with Soil possessing the greater frequency (Appendix 3, Table 3.1).

Table 6.2 Frequency (all sites) of each species across each substrate for each size class. DaC, *D. antarctica* caudex; FC, fallen *D. antarctica* caudex; CWD, Coarse woody debris; Soil, Soil and litter; Cop, Coppice.

Substrate	Frequency		
	< 0.2 m tall	≥ 0.2 to < 3 m tall	≥ 3 m tall
<i>Atherosperma moschatum</i>			
DaC	52	29	32
FC	701	3	16
CWD	1084	0	6
Soil	153	4	70
Copp	58	48	113
Total	2048	84	237
<i>Coprosma quadrifida</i>			
DaC	59	18	0
FC	97	0	0
CWD	289	0	0
Soil	1838	36	5
Copp	0	0	0
Total	2283	54	5
<i>Nothofagus cunninghamii</i>			
DaC	64	14	15
FC	261	0	4
CWD	422	3	7
Soil	528	10	137
Copp	38	12	37
Total	1313	39	190
<i>Olearia argophylla</i>			
DaC	275	12	4
FC	145	0	0
CWD	278	0	0
Soil	329	6	87
Copp	0	0	0
Total	1027	18	91
<i>Pittosporum bicolor</i>			
DaC	113	77	23
FC	67	1	2
CWD	182	1	0
Soil	704	26	30
Copp	0	0	0
Total	1066	105	55
<i>Tasmannia lanceolata</i>			
DaC	54	47	6
FC	48	2	6
CWD	39	5	1
Soil	98	1	50
Copp	0	0	0
Total	239	55	63

Erect *Dicksonia antarctica* caudices supported a greater frequency of *Pittosporum bicolor* seedlings (< 0.20 m tall) than either FC or CWD. Both DaC and Soil supported similar frequencies of *Pittosporum bicolor* seedlings, but soil's frequency was not different to that of CWD. Erect *D. antarctica* caudices (DaC) supported the greatest frequency of established (≥ 0.2 to < 3 m tall) *Pittosporum bicolor* out of all the substrates. However, soil supported a greater frequency of established *Pittosporum bicolor* than either FC or CWD. The combined frequency of established *Pittosporum bicolor* on elevated substrates was greater than Soil. Erect *Dicksonia antarctica* caudices and Soil supported similar frequencies of mature (≥ 3 m tall) *Pittosporum bicolor* and both were greater than either FC or CWD (Appendix 3, Table 3.1).

Dicksonia antarctica caudices (DaC), fallen *D. antarctica* caudices (FC), coarse woody debris (CWD) and Soil supported similar frequencies of *Tasmannia lanceolata* seedlings (< 0.20 m tall). Established (≥ 0.20 to < 3 m tall) *Tasmannia lanceolata* occurred predominantly on DaC, with FC, CWD and Soil supporting similar frequencies. The combined frequency of established *Tasmannia lanceolata* on elevated substrates was greater than that of Soil. The frequency of mature (≥ 3 m tall) *Tasmannia lanceolata* on DaC, FC, CWD and Soil were similar to each other (Appendix 3, Table 3.1).

Where found as epiphytes on *D. antarctica*, *Atherosperma moschatum*, *Nothofagus cunninghamii*, *Tasmannia lanceolata* and *Olearia argophylla* occurred predominantly on the section of the caudex with a rough texture (Table 6.3). Seedlings (< 0.20 m tall) of *Coprosma quadrifida* and *Pittosporum bicolor* occurred predominantly on the rough surface of the caudex, however established/mature (≥ 0.20 m tall) individuals occurred at similar frequencies on each of the three caudex textures (rough, irregular and frizzy) (Table 6.3).

Table 6.3 Kruskal-Wallis test results (adjusted for ties) α 0.05. Comparison of facultative epiphyte species frequencies rooted in the different *D. antarctica* caudex surface texture classes, Rough texture, Irregular texture and Frizzy texture.

Species	Caudex texture class	Average rank	Z	Result
<i>Atherosperma moschatum</i> < 0.20 m tall	Rough	1439.5	0.85	H = 30.09 df = 2 p ≤ 0.001
	Irregular	1411.0	-0.46	
	Frizzy	1412.5	-0.39	
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	Rough	1451.0	1.38	H = 47.07 df = 2 p ≤ 0.001
	Irregular	1407.5	-0.62	
	Frizzy	1404.5	-0.76	
<i>Nothofagus cunninghamii</i> < 0.20 m tall	Rough	1511.0	1.08	H = 35.93 df = 2 p ≤ 0.001
	Irregular	1478.0	-0.40	
	Frizzy	1472.0	-0.67	
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	Rough	1493.5	0.29	H = 7.04 df = 2 p = 0.030
	Irregular	1486.0	-0.04	
	Frizzy	1472.0	-0.67	
<i>Coprosma quadrifida</i> < 0.20 m tall	Rough	1029.6	1.23	H = 32.17 df = 2 p ≤ 0.001
	Irregular	1002.4	-0.25	
	Frizzy	989.0	-0.98	
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	Rough	1005.5	-0.08	H = 0.40 df = 2 p = 0.818
	Irregular	1007.0	-0.00	
	Frizzy	1008.5	0.08	
<i>Pittosporum bicolor</i> < 0.20 m tall	Rough	1713.0	0.48	H = 6.53 df = 2 p = 0.038
	Irregular	1693.5	-0.34	
	Frizzy	1698.0	-0.15	
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	Rough	1704.4	0.12	H = 0.28 df = 2 p = 0.869
	Irregular	1698.5	-0.12	
	Frizzy	1701.5	0.00	
<i>Tasmannia lanceolata</i> < 0.20 m tall	Rough	1351.0	0.59	H = 13.72 df = 2 p = 0.001
	Irregular	1339.0	0.02	
	Frizzy	1325.5	-0.61	
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	Rough	1353.6	0.71	H = 13.47 df = 2 p ≤ 0.001
	Irregular	1333.9	-0.22	
	Frizzy	1328.0	-0.50	
<i>Olearia argophylla</i> < 0.20 m tall	Rough	1484.2	2.41	H = 68.74 df = 2 p ≤ 0.001
	Irregular	1414.9	-0.76	
	Frizzy	1395.5	-1.65	
<i>Olearia argophylla</i> ≥ 0.20 m tall	Rough	1437.5	0.27	H = 6.53 df = 2 p = 0.038
	Irregular	1437.5	-0.21	
	Frizzy	1430.0	-0.07	

The separate frequencies of all facultative epiphyte species either as seedlings (< 0.20 m tall) or as established/mature specimens (≥ 0.20 m tall) were similar among the four aspect classes of the *D. antarctica* caudex surface (Table 6.4).

Except for established (≥ 0.20 to < 3 m tall) *Nothofagus cunninghamii* (Table 6.5), which showed larger frequencies on sites classed as high fertility there was no variation in any frequencies of any epiphyte species between the high and low site fertility classes.

Table 6.4 Kruskal-Wallis test results (adjusted for ties) α 0.05. Comparison of the frequency of common facultative epiphyte species rooted in *D. antarctica* caudices at differing aspects on the caudex (1 = North, 2 = East, 3 = South and 4 = West).

Frequency	Aspect class	Result
<i>Atherosperma moschatum</i> < 0.20 m tall	All	H = 2.43 df = 3 p = 0.488
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	All	H = 1.06 df = 3 p = 0.788
<i>Nothofagus cunninghamii</i> < 0.20 m tall	All	H = 3.22 df = 3 p = 0.359
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	All	H = 1.20 df = 3 p = 0.754
<i>Coprosma quadrifida</i> < 0.20 m tall	All	H = 2.02 df = 3 p = 0.567
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	All	H = 5.04 df = 3 p = 0.169
<i>Pittosporum bicolor</i> < 0.20 m tall	All	H = 4.37 df = 3 p = 0.224
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	All	H = 0.57 df = 3 p = 0.903
<i>Tasmannia lanceolata</i> < 0.20 m tall	All	H = 5.33 df = 3 p = 0.149
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	All	H = 3.07 df = 3 p = 0.382
<i>Olearia argophylla</i> < 0.20 m tall	All	H = 0.96 df = 3 p = 0.810
<i>Olearia argophylla</i> ≥ 0.20 m tall	All	H = 1.27 df = 3 p = 0.736

Table 6.5 Kruskal-Wallis test results (adjusted for ties) α 0.05. Comparison among the site fertility classes of the frequency of common facultative epiphyte species in each size class (< 0.20 m tall, \geq 0.20 to < 3 m tall and \geq 3 m tall) rooted in soil.

Frequency on soil	Fertility class	Average rank	Result
<i>Atherosperma moschatum</i> < 0.20 m tall	1	ns	H = 0.03 df = 1
	2	ns	p = 0.874
<i>Atherosperma moschatum</i> \geq 0.20 to < 3 m tall	1	ns	H = 0.167 df = 1
	2	ns	p = 0.197
<i>Atherosperma moschatum</i> \geq 3 m tall	1	ns	H = 1.20 df = 1
	2	ns	p = 0.274
<i>Nothofagus cunninghamii</i> < 0.20 m tall	1	ns	H = 0.00 df = 1
	2	ns	p = 1.00
<i>Nothofagus cunninghamii</i> \geq 0.20 to < 3 m tall	1	8.0	H = 3.90 df = 1
	2	10.8	p = 0.48
<i>Nothofagus cunninghamii</i> \geq 3 m tall	1	ns	H = 0.57 df = 1
	2	ns	p = 0.449
<i>Coprosma quadrifida</i> < 0.20 m tall	1	ns	H = 0.02 df = 1
	2	ns	p = 0.876
<i>Coprosma quadrifida</i> \geq 0.20 m tall	1	ns	H = 1.69 df = 1
	2	ns	p = 0.193
<i>Pittosporum bicolor</i> < 0.20 m tall	1	ns	H = 2.08 df = 1
	2	ns	p = 0.149
<i>Pittosporum bicolor</i> \geq 0.20 to < 3 m tall	1	ns	H = 1.17 df = 1
	2	ns	p = 2.79
<i>Pittosporum bicolor</i> \geq 3 m tall	1	ns	H = 0.99 df = 1
	2	ns	p = 0.321
<i>Tasmannia lanceolata</i> < 0.20 m tall	1	ns	H = 1.00 df = 1
	2	ns	p = 0.318
<i>Tasmannia lanceolata</i> \geq 0.20 to < 3 m tall	1	ns	H = 0.27 df = 1
	2	ns	p = 0.602
<i>Tasmannia lanceolata</i> \geq 3 m tall	1	ns	H = 1.37 df = 1
	2	ns	p = 0.242
<i>Olearia argophylla</i> < 0.20 m tall	1	ns	H = 0.00 df = 1
	2	ns	p = 0.951
<i>Olearia argophylla</i> \geq 0.20 to < 3 m tall	1	ns	H = 2.24 df = 1
	2	ns	p = 0.134
<i>Olearia argophylla</i> \geq 3 m tall	1	ns	H = 3.35 df = 1
	2	ns	p = 0.067

The two facultative epiphyte size classes, i.e. seedling (< 0.20 m tall) and established/mature (\geq 0.20 m tall) differed in their observed attachment height on *D. antarctica* caudices for each of the facultative epiphyte species included in the analysis (Table 6.6). For each facultative epiphyte species, established/mature individuals were attached predominantly higher on *D. antarctica* caudices than were the seedlings.

The height of established (\geq 0.20 m tall) *Nothofagus cunninghamii* observed growing on *D. antarctica* caudices is similar to that of established *Pittosporum bicolor* and established *Tasmannia lanceolata* (Table 6.7). Established *Atherosperma moschatum*, *Pittosporum bicolor* and *Tasmannia lanceolata* all occurred at similar heights on *D. antarctica* caudices (Table 6.7). Established *Atherosperma moschatum* and *Coprosma quadrifida* both occurred at similar heights on *D. antarctica* caudices. Established *Coprosma quadrifida* and *Olearia argophylla* also occurred at similar heights on *D. antarctica* caudices (Table 6.7).

Table 6.6 Kruskal-Wallis test results (adjusted for ties) α 0.05. Comparison among size classes (< 0.20 m tall and \geq 0.20 m tall) of above ground height at which common facultative epiphytes are rooted in *D. antarctica* caudices (for each species).

Species	Size class	Median height above ground	Result
<i>Atherosperma moschatum</i>	< 0.20 m tall	0.82 m	H = 23.21 df = 1 $p \leq 0.001$
	\geq 0.20 m tall	1.38 m	
<i>Nothofagus cunninghamii</i>	< 0.20 m tall	0.34 m	H = 41.77 df = 1 $p \leq 0.001$
	\geq 0.20 m tall	1.96 m	
<i>Coprosma quadrifida</i>	< 0.20 m tall	0.18 m	H = 18.58 df = 1 $p \leq 0.001$
	\geq 0.20 m tall	1.35 m	
<i>Pittosporum bicolor</i>	< 0.20 m tall	1.39 m	H = 8.75 df = 1 $p = 0.003$
	\geq 0.20 m tall	1.74 m	
<i>Tasmannia lanceolata</i>	< 0.20 m tall	1.42 m	H = 11.06 df = 1 $p \leq 0.001$
	\geq 0.20 m tall	1.60 m	
<i>Olearia argophylla</i>	< 0.20 m tall	0.53 m	H = 3.99 df = 1 $p = 0.046$
	\geq 0.20 m tall	1.00 m	

Table 6.7 Kruskal-Wallis test results (adjusted for ties) α 0.05. Comparison of the height above ground on *D. antarctica* caudices among each common facultative epiphyte species in size class \geq 0.2 m.

Height above ground on <i>D. antarctica</i> Caudices	Average Rank	Result
<i>Atherosperma moschatum</i> \geq 0.20 m tall	45.4	H = 3.63 df = 1 p = 0.05
<i>Nothofagus cunninghamii</i> \geq 0.20 m tall	57.9	
<i>Atherosperma moschatum</i> \geq 0.20 m tall	47.1	H = 2.35 df = 1 p = 0.125
<i>Coprosma quadrifida</i> \geq 0.20 m tall	37.6	
<i>Atherosperma moschatum</i> \geq 0.20 m tall	81.1	H = 1.73 df = 1 p = 0.189
<i>Pittosporum bicolor</i> \geq 0.20 m tall	91.2	
<i>Atherosperma moschatum</i> \geq 0.20 m tall	59.0	H = 2.09 df = 1 p = 0.149
<i>Tasmannia lanceolata</i> \geq 0.20 m tall	68.5	
<i>Atherosperma moschatum</i> \geq 0.20 m tall	46.7	H = 4.76 df = 1 p = 0.029
<i>Olearia argophylla</i> \geq 0.20 m tall	31.1	
<i>Nothofagus cunninghamii</i> \geq 0.20 m tall	25.9	H = 7.19 df = 1 p = 0.007
<i>Coprosma quadrifida</i> \geq 0.20 m tall	15.6	
<i>Nothofagus cunninghamii</i> \geq 0.20 m tall	70.9	H = 1.43 df = 1 p = 0.232
<i>Pittosporum bicolor</i> \geq 0.20 m tall	61.1	
<i>Nothofagus cunninghamii</i> \geq 0.20 m tall	42.0	H = 0.62 df = 1 p = 0.432
<i>Tasmannia lanceolata</i> \geq 0.20 m tall	37.7	
<i>Nothofagus cunninghamii</i> \geq 0.20 m tall	24.1	H = 8.01 df = 1 p = 0.005
<i>Olearia argophylla</i> \geq 0.20 m tall	13.5	
<i>Coprosma quadrifida</i> \geq 0.20 m tall	41.1	H = 6.21 df = 1 p = 0.013
<i>Pittosporum bicolor</i> \geq 0.20 m tall	63.1	
<i>Coprosma quadrifida</i> \geq 0.20 m tall	26.0	H = 5.69 df = 1 p = 0.017
<i>Tasmannia lanceolata</i> \geq 0.20 m tall	39.4	
<i>Coprosma quadrifida</i> \geq 0.20 m tall	18.2	H = 0.63 df = 1 p = 0.426
<i>Olearia argophylla</i> \geq 0.20 m tall	15.5	
<i>Pittosporum bicolor</i> \geq 0.20 m tall	76.7	H = 0.09 df = 1 p = 0.765
<i>Tasmannia lanceolata</i> \geq 0.20 m tall	79.0	
<i>Pittosporum bicolor</i> \geq 0.20 m tall	62.0	H = 8.22 df = 1 p = 0.004
<i>Olearia argophylla</i> \geq 0.20 m tall	35.3	
<i>Tasmannia lanceolata</i> \geq 0.20 m tall	37.9	H = 7.09 df = 1 p = 0.008
<i>Olearia argophylla</i> \geq 0.20 m tall	22.5	

The combined frequency of established (≥ 0.20 to < 3 m) *Atherosperma moschatum* on all substrates was negatively correlated with the mid-class foliage projective cover (FPC) value of ground cover. The combined mid-class FPC value (as outlined in Chapter 3) of ground cover and lower understorey was positively correlated with the combined substrate frequencies of *Coprosma quadrifida* seedlings (< 0.20 m tall) and established *Coprosma quadrifida*. The combined substrate frequency of established *Tasmannia lanceolata* was negatively correlated with the mid-class FPC value of ground cover and the combined mid-class FPC value of ground cover and lower understorey. The combined frequency of *Olearia argophylla* seedlings observed across all substrates was negatively correlated with the combined mid-class FPC value of the lower understorey, high understorey, subcanopy and canopy as well as with the combined mid-class FPC value of the high understorey, subcanopy and canopy (Appendix 6, Table 6.1).

Histograms of the distribution of facultative epiphyte attachment heights (above ground) on *D. antarctica* caudices are displayed in Figure 6.1. There are separate histograms for each species in each facultative epiphyte size class of seedling (< 0.20 m tall) and established/mature (≥ 0.20 m tall).

The frequencies of seedling (< 0.20 m tall) and established/mature (≥ 0.20 m tall) *Atherosperma moschatum* and the combination of both frequencies on *D. antarctica* caudices are each positively correlated with *D. antarctica* erect caudex length, *D. antarctica* maximum diameter and *D. antarctica* rough caudex surface length respectively (Appendix 4, Table 4.1). *Atherosperma moschatum* frequencies for both size classes on erect *D. antarctica* caudices (DaC) are positively correlated with *D. antarctica* crown area index (CAI) and frond frequency respectively. The frequency of *Atherosperma moschatum* seedlings on DaC is negatively correlated with residual frond frequency.

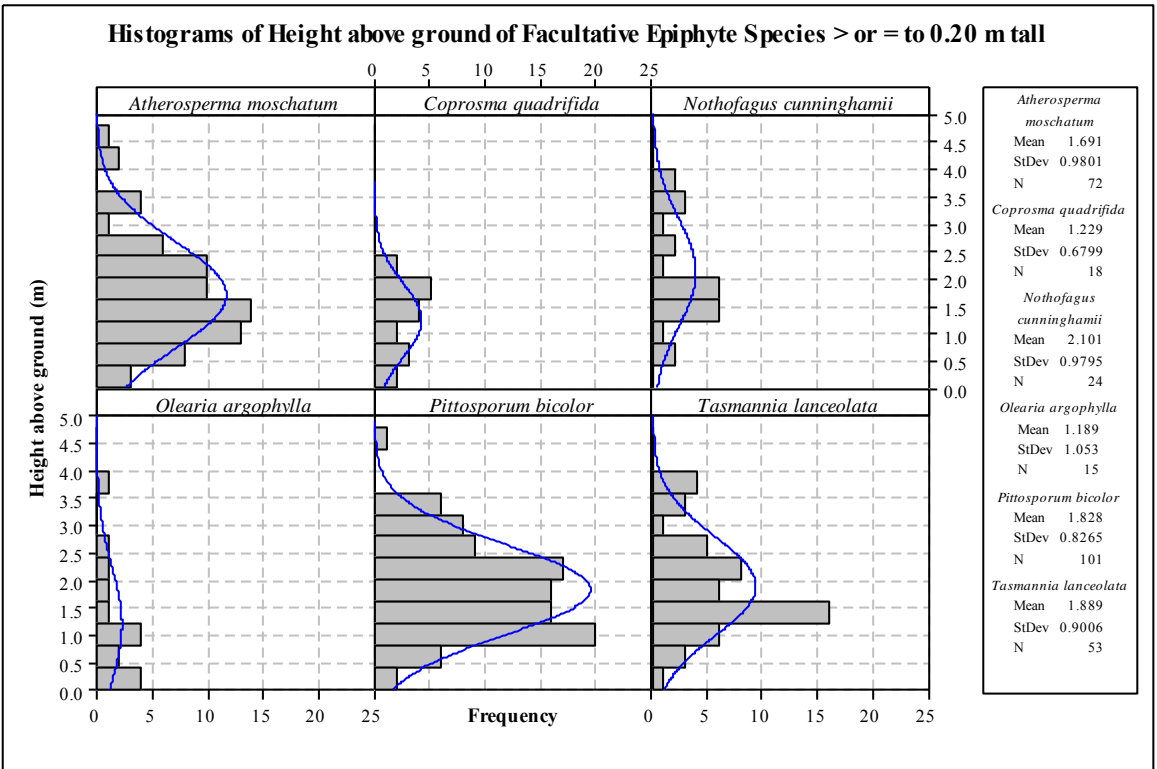
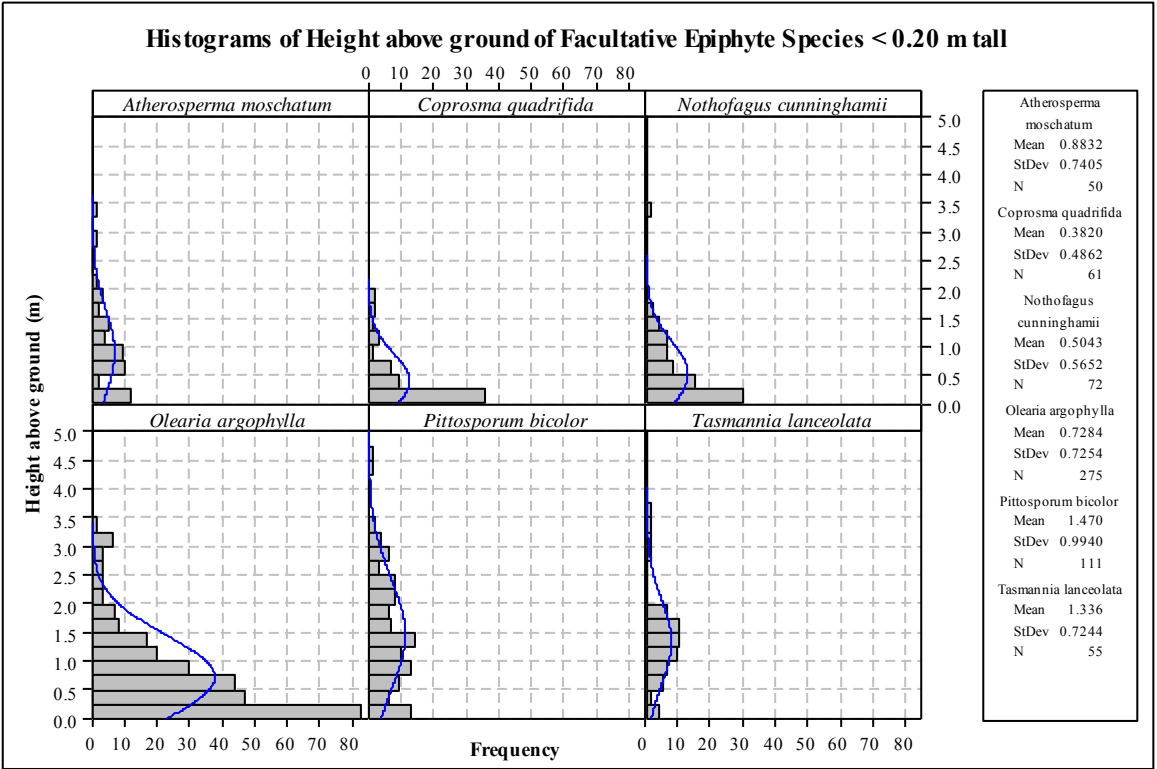


Figure 6.1 Histograms showing the distribution of facultative epiphyte attachment heights from the ground on *D. antarctica* caudices. There are separate histograms for each species in each facultative epiphyte size class (i.e. < 0.20 m tall and \geq 0.20 m tall). Frequencies and heights on caudices are from all sample sites.

The frequencies of seedling (< 0.20 m tall) and established/mature (≥ 0.20 m tall) *Nothofagus cunninghamii* and the combination of both observed on *D. antarctica* caudices are each positively correlated with *D. antarctica* erect caudex length (Appendix 4, Table 4.1). The frequency of seedling *Nothofagus cunninghamii* observed on *D. antarctica* caudices is positively correlated with *D. antarctica* maximum diameter and *D. antarctica* rough caudex length. The combined frequency of seedling (< 0.20 m tall) and established/mature (≥ 0.20 m tall) *Nothofagus cunninghamii* is also correlated with *D. antarctica* maximum diameter and *D. antarctica* rough caudex length respectively.

The frequency of *Coprosma quadrifida* seedlings (< 0.20 m tall) and the combined frequencies of seedlings and established/mature specimens (≥ 0.20 m tall) recorded on *D. antarctica* caudices are positively correlated with *D. antarctica* erect length, *D. antarctica* rough caudex length and residual frond frequency respectively (Appendix 4, Table 4.1).

The frequencies of *Pittosporum bicolor* seedlings (< 0.20 m tall) and established/mature specimens (≥ 0.20 m tall) as well as the combined frequencies of seedlings and established/mature specimens recorded on erect *D. antarctica* caudices (DaC) are positively correlated with *D. antarctica* erect length, *D. antarctica* maximum diameter and *D. antarctica* rough caudex length (Appendix 4, Table 4.1). The frequencies of *Pittosporum bicolor* seedlings (≥ 0.20 m tall) and the combined frequency of seedlings and established/mature specimens recorded on DaC are positively correlated with *D. antarctica* crown area index (CAI) and frond frequency. The combined frequency of *Pittosporum bicolor* seedlings and established/mature specimens recorded on DaC is positively correlated with *D. antarctica* residual frond frequency (Appendix 4, Table 4.1).

The frequencies of *Tasmannia lanceolata* seedlings (< 0.20 m tall) and established/mature specimens (≥ 0.20 m tall) as well as the combined frequencies of seedlings and established/mature specimens recorded on DaC are positively correlated with *D. antarctica* erect length, *D. antarctica* maximum diameter, *D. antarctica* rough caudex length and

frond frequency (Appendix 4, Table 4.1). The frequency of *Tasmannia lanceolata* seedlings and the combined frequencies of both seedlings and established/mature specimens recorded on DaC are positively correlated with CAI.

The frequencies of *Olearia argophylla* seedlings (< 0.20 m tall) and established/mature specimens (≥ 0.20 m tall) as well as the combined frequencies of both seedlings and established/mature specimens on *D. antarctica* caudices (DaC) are positively correlated with *D. antarctica* erect length, *D. antarctica* maximum diameter and *D. antarctica* rough caudex length respectively (Appendix 4, Table 4.1). The frequencies of *Olearia argophylla* seedlings and the combined frequencies of both seedlings and established/mature specimens recorded on DaC are positively correlated with *D. antarctica* crown area index (CAI), frond frequency and residual frond frequency respectively (Appendix 4 Table 4.1).

Large (erect caudex length ≥ 3 m) *D. antarctica* supported the greater numbers of epiphytic *Atherosperma moschatum*, *Nothofagus cunninghamii*, *Pittosporum bicolor* and *Tasmannia lanceolata* compared with the other two caudex size classes (erect caudex length < 2 m and ≥ 2 m to < 3 m) (Appendix 5, Table 5.1). The greater *Coprosma quadrifida* frequency occurred on mid-sized (erect caudex length ≥ 2 m to < 3 m) *D. antarctica*. The greater *Olearia argophylla* frequency occurred on *D. antarctica* caudices in the two larger size classes (erect caudex length ≥ 2 m to < 3 m and ≥ 3 m) (Appendix 5 Table 5.1).

Discussion

Thirty-two typically terrestrial plant species, excluding shootless apogeotropic roots, were identified as rooted in caudices of *D. antarctica*, of which 22 were represented in part by mature or near mature individuals and 10 (all large tree or shrub species) by established juveniles (Table 6.1 and Figure 6.2 for an example). Although juveniles had yet to show reproductive success, the *D. antarctica* caudex-soil continuum greatly increases their potential to become rooted in the ground. Contact with the larger nutrient reservoir of the soil should provide juveniles with the resources necessary to achieve reproductive success

given time. Based on this assumption, 28 primarily terrestrial species are facultative epiphytes of *D. antarctica*. The 4 remaining species (Table 6.1) which are *Histiopteris incisa* (Thunb.) J.Sm., *Hydrocotyle hirta* R.Br. ex A.Rich., *Hypolepis rugosula* (Labill.) J.Sm., and *Pteridium esculentum* (G.Forst.) Cockayne, have come to be rooted in the caudex of *D. antarctica* by apparently growing into the root mantle from the soil. These soil



Figure 6.2 A *D. antarctica* caudex host to *Atherosperma moschatum* (arrow), *Nothofagus cunninghamii* (arrow) and *Gaultheria hispida* (arrow). Although not evident in this image the same caudex also hosted *Coprosma quadrifida*, *Pittosporum bicolor* and *Tasmannia lanceolata*. The same caudex is shown from a different angle in Figure 1.4.

sourced species are termed facultative secondary hemi-epiphytes (Benzing 2008, Moffett 2000). Germinates of *Acacia* spp. were present epiphytically on *D. antarctica*, at several sites, but were only identifiable to the generic level. Assuming the *Acacia* spp. germinates are the same species as nearby mature individuals then they would be *Acacia dealbata* Link, *Acacia mearnsii* De Wild., or *Acacia melanoxylon*, depending on the site. Out of these only *Acacia melanoxylon* was present as a mature epiphyte, meaning *Acacia dealbata* and *Acacia mearnsii* are potentially accidental epiphytes within this broad range of sites as there is no evidence that they establish to maturity on *D. antarctica* caudices in this study. *Acacia dealbata* and *Acacia mearnsii* are pioneer species and have a much lower shade tolerance than *Acacia melanoxylon*, which probably explains their absence as mature facultative epiphytes in the forest understorey.

Although *D. antarctica* caudices are not a singularly dominant germination substrate for any of the seven common facultative epiphyte species observed in this study, they are a codominant germination substrate for *Atherosperma moschatum*, *Olearia argophylla*, *Pittosporum bicolor*, and *Tasmannia lanceolata* (Appendix 3, Table 3.1). It is concluded therefore that *D. antarctica* caudices are important germination substrates for these species in moist forests of north-east Tasmania. *Nothofagus cunninghamii* showed no clear preference for any one germination substrate although the results suggest coarse woody debris and to a lesser extent the soil are important (Appendix 3 Table 3.1). Coarse woody debris (CWD) has been identified by other authors as a critical germination substrate for *Nothofagus cunninghamii* (Howard 1973a, McKenny and Kirkpatrick 1999).

Coprosma quadrifida showed a preference for soil over the other available substrates especially in the smaller (< 0.20 m tall) size class (Appendix 3 Table 3.1), perhaps due to its branches terminating in fine spines (Figure 6.3), as pruning by herbivores promotes branching and the number of new spines, which in turn protect the plant (Curtis 1963). Excessive herbivory of small *Coprosma quadrifida* appears to lead to the formation of well developed spiny bonsai-like individuals that are usually less than 0.20 m high. In this

manner, soil rooted *Coprosma quadrifida* survive browsing, however recruitment into the larger height class is reduced while the relative frequency of individuals in the smaller (< 0.20 m tall) height class is increased. Bonsai-like *Coprosma quadrifida* were rarely observed on *D. antarctica* caudices, but larger-sized (taller) *Coprosma quadrifida* were observed frequently on *D. antarctica* caudices, suggesting they are thus out of reach of regular browsers.



Figure 6.3 *Coprosma quadrifida* (arrow) growing epiphytically on a *D. antarctica* caudex.

Three characteristics of *D. antarctica* may serve to enhance the retention and colonisation of suitable seeds on the caudex of the ferns, resulting in the facultative epiphyte frequencies observed here. The tree fern's apical frond rosette may intercept and funnel anemochorous seed of *Atherosperma moschatum*, *Nothofagus cunninghamii* and *Olearia argophylla* onto the *D. antarctica* caudex from across a wider catchment area than the caudex alone would intercept. Secondly the irregularly fluted and creviced texture of *D. antarctica* caudices may increase the frequency with which anemochorous seed lodges in the caudex. Gaxiola

et al. (2008) identified a similar situation with another species of *Dicksonia*, *D. squarrosa* in New Zealand.

Erect *Dicksonia antarctica* caudices also provides a likely avian perching and/or nesting site. *Dicksonia antarctica* rosette sites that are preferred by birds may receive greater faecal deposition of seeds and other material than other nearby substrates. Since the presence of undamaged *Coprosma quadrifida* and *Pittosporum bicolor* seed has been identified in the faeces of frugivorous birds (French 1990), there is the potential for seed of these two species and possibly *Tasmannia lanceolata* to become concentrated on and around *D. antarctica* caudices. Soil has the larger surface area compared to the total caudex surface area in each plot and yet there is no significant variation between the frequencies of *Atherosperma moschatum*, *Nothofagus cunninghamii*, *Olearia argophylla*, *Pittosporum bicolor* and *Tasmannia lanceolata* seedlings (< 0.20 m tall) respectively on *D. antarctica* caudices and on the soil (Appendix 3, Table 3.1). This suggests that the seed of these species are concentrated disproportionately in favour of the caudex and/or that the caudex is a superior germination medium for these species.

All seven common facultative epiphyte species indicated significantly greater frequencies of seedlings that were rooted in the rough textured surfaces of the caudex, relative to the other caudex textures viz. irregular, frizzy and apical debris ring (Table 6.3). The presence of a deeply fissured substrate and potentially greater nutrient and moisture reservoir in sections of the caudex with a rough surface may explain the increased frequency of epiphytes compared to other surface textures. Coupled with this would be the tendency of seeds intercepted or deposited in arboreal faeces, but not restrained in the upper sections of the caudex, to gravitate/fall downwards and lodge in the lower and wider sections of the caudex. The rough textured surfaces of a *D. antarctica* caudex always occur on the lowest and widest sections of the caudex (Chapter 4). This may also provide the preferred humidity conditions for germination, nearest to the ground.

High vs. low site fertility class was not observed to be associated with differences in the frequency of any of the observed epiphyte species found growing on soil substrate, in any size class, except for *Nothofagus cunninghamii* (Table 6.5). However, variations in substrate nutrient availability have been suggested as a cause of differences in growth rate, but not frequency, among seedlings rooted in soil and tree fern caudices (Bellingham and Richardson 2006, Gaxiola *et al.* 2008). In some instances where topography and/or pedogenic processes limit soil nutrient availability, tree fern caudices may contain sufficient substrate retention and on-going nutrition for the growth rate of facultative epiphyte seedlings to surpass that of seedlings rooted in the soil (Bellingham and Richardson 2006, Gaxiola *et al.* 2008). Nevertheless it does not seem feasible that even a sizeable *D. antarctica* caudex could contain adequate nutrition for larger facultative epiphyte species, e.g. trees, to reach canopy height without access to a greater and longer lasting nutrient reservoir. Elsewhere, the comparatively huge accumulations of canopy soil (i.e. humus) and decaying organic matter retained in the canopy of mature *Sequoia sempervirens* (redwood) still leads to the dwarfing of facultative and accidental epiphyte tree species (Preston 2007). It appears that larger facultative epiphyte species hosted by tree ferns must therefore become nutritionally independent of their host and root in the soil before they can attain appreciable size.

Atherosperma moschatum, *Pittosporum bicolor*, and *Tasmannia lanceolata*

In undisturbed mature wet forests of north-east Tasmania, *Atherosperma moschatum*, *Pittosporum bicolor*, and *Tasmannia lanceolata* seedlings preferentially established on large (mature) *D. antarctica* caudices (Figure 6.4 and Figure 6.5), as opposed to other available substrates of soil/litter, fallen *D. antarctica*, and coarse woody debris (CWD) (Appendix 3 Table 3.1). Large *D. antarctica* caudices are therefore a critical substrate component of a mature wet forest understorey if observed population sizes of *Pittosporum bicolor* and *Tasmannia lanceolata* are to be maintained. Since populations of *Atherosperma moschatum* can regenerate vegetatively by coppicing they are not totally reliant on *D. antarctica* caudices to maintain population size. Instead, large *D. antarctica* caudices



Figure 6.4 Image of *Atherosperma moschatum* (arrow) and *Nothofagus cunninghamii* (arrow) that have established on the caudex of a *D. antarctica*.

improve *Atherosperma moschatum* genetic diversity by providing a site for seed germination and seedling establishment and thereby discouraging the dominance of coppice, which itself can lead to reduced genetic diversity and potential inbreeding (Shapcott 1994).

Browsing pressure is a possible agent selecting against the establishment of *Atherosperma moschatum*, *Pittosporum bicolor*, and *Tasmannia lanceolata* on forest floor substrates. Hickey (1982) and Neyland (1991) identified that mammalian browsing limited *Atherosperma moschatum* regeneration under a closed forest canopy in Tasmania. *Pittosporum bicolor* has also been observed as a favourite of browsers (Hickey 1982, McLeod and Gray 2005, Neyland 1991). *Tasmannia lanceolata* on the other hand contains the chemical polygodial in its leaves, an insecticidal anti-feedant (Munoz-Concha *et al.* 2007), and this has been hypothesized to deter browsing (Read and Menary 2000), although direct evidence is lacking and this explanation may be negated if extant herbivores coevolved with *Tasmannia lanceolata*.



Figure 6.5 Image of *Tasmannia lanceolata* (arrow) and *Pittosporum bicolor* (arrow) that have established on the caudex of a *D. antarctica*.

Further evidence of browsing pressure is provided by the significantly higher attachment positions of established/mature (≥ 0.20 m tall) *Atherosperma moschatum*, *Pittosporum bicolor*, and *Tasmannia lanceolata* on *D. antarctica* caudices compared to the attachment positions of seedlings (< 0.20 m tall) of the same species (Table 6.6 and Figure 6.1). Increased browsing removal of plants within reach of browsers on *D. antarctica* caudices could explain the observed height differential. If the selecting agent is mammalian browsing then the similar heights of attachment of established (≥ 0.2 to < 3 m tall) *Atherosperma moschatum*, *Pittosporum bicolor*, and *Tasmannia lanceolata* on *D. antarctica* caudices suggests a similarly sized or common browser (Table 6.7). Greater exposure to light with increasing height on a *D. antarctica* caudex would also contribute to the greater establishment success of plants higher off the ground, especially in heavily shaded understories where sunlight may be limiting for canopy opportunists. However there is no relationship between foliage projective cover (FPC) of the separate and combined canopy strata (high understorey, subcanopy and canopy only) and the frequencies of *Atherosperma moschatum*, *Pittosporum bicolor*, or *Tasmannia lanceolata* in any size class on any substrate (Appendix 6, Table 6.1). Juvenile *Atherosperma moschatum* can tolerate low light levels, which may explain the lack of a relationship between its observed frequency and foliage projective cover. However, the relationships between understorey irradiance and growth rates of *Pittosporum bicolor* and *Tasmannia lanceolata* are not known.

Nothofagus cunninghamii

The low shade tolerance of *Nothofagus cunninghamii* (Read 1982, Read and Brown 1996) (Figure 6.6) restricts its non-vegetative regeneration to sunlit environments, such as canopy gaps and elevated substrates (Howard 1973a). Insolation is important not just for growth, *per se*, but to enable a seedling to reach a size where it is less vulnerable to threats, as quickly as possible (Howard 1973b). The lack of significant variation between the frequencies of established (≥ 0.2 to < 3 m tall) *Nothofagus cunninghamii* among all four substrates (Appendix 3, Table 3.1) suggests that establishment of this canopy species (in

undisturbed forest) is not restricted to any one substrate, but occurs across all substrates, provided there is the opportunity for sufficient sunlight and nutrition. The significantly higher attachment positions of established (≥ 0.20 m tall) *Nothofagus cunninghamii* on *D. antarctica* caudices compared to the lower attachment positions of seedlings (< 0.20 m tall) of the same species (Table 6.6 and Figure 6.1) may be due to increasing insolation with height above ground, however the current research did not measure irradiance in the forest canopy or understorey. In contrast to *Atherosperma moschatum* browsing pressure is an unlikely cause of the height differential observed in *Nothofagus cunninghamii* due to the comparatively reduced palatability of the



Figure 6.6 Image of *Nothofagus cunninghamii* seedlings (arrow) that have established low on the caudex of *D. antarctica*.

foliage. *Nothofagus cunninghamii* has low foliar nutrient value (per gram dry weight) and a high anti-feedant and anti-digestant concentration in its leaves (Read and Brown 1996). Although extant coevolved species may be able to browse *Nothofagus cunninghamii* foliage, research by Hickey (1982) identified that this tree species has a low browsing index compared to co-occurring species.

McKenny and Kirkpatrick (1999) suggested some seedlings, including *Nothofagus cunninghamii*, have an increased establishment success on fallen logs (i.e. CWD) compared to the soil, because the greater height and bulk density of some CWD reduce the occurrence of root competition and vertebrate bioturbation. The current research results differ from that of McKenny and Kirkpatrick (1999) as there is no significant variation of established (≥ 0.2 to < 3 m tall) *Nothofagus cunninghamii* frequencies among the four substrates tested (Appendix 3, Table 3.1). The difference in observations is potentially due to the absence of introduced *Menura novae-hollandiae* (Lyrebirds) in north-east Tasmania but not from the southern Tasmanian field sites of the McKenny and Kirkpatrick (1999) study. It has been estimated that Lyrebirds turn over the forest floor every 1-2 years making it difficult for seedlings to become established on exposed soil microsites (McKenny and Kirkpatrick 1999).

Olearia argophylla

Olearia argophylla seedlings were prolific throughout the study sites, with *D. antarctica* caudices and soil being the dominant germination substrates (Appendix 3, Table 3.1). However, there is a dramatic drop in the frequency of *Olearia argophylla* between seedlings (< 0.20 m tall) and established plants (≥ 0.20 m to < 3 m tall), across all substrates (and Figure 6.1). This represents poor establishment success of *Olearia argophylla* in the conditions represented in the study sites. The negative Spearman's rho correlation of -0.518, ($p = 0.04$) for the frequency of *Olearia argophylla* seedlings (< 0.20 m tall) versus combined canopy/subcanopy foliage cover (FPC) suggests that canopy closure inhibits regeneration of *Olearia argophylla* by reducing sunlight infiltration or other competitive influence (Appendix 6, Table 6.1). This suggests young *Olearia argophylla* are essentially shade intolerant and hence a pioneer, gap opportunist and edge species. This result is in agreement with Neyland (1991) who observed a greater frequency of *Olearia argophylla* under a broken canopy, e.g. in wet eucalypt forest where it is common, compared with its rarity in undisturbed rainforest.

Large (≥ 3 m tall) *Olearia argophylla* are present throughout the study area in higher densities than those of lesser size (≥ 0.2 to < 3 m tall), however soil is the dominant substrate, ahead of *D. antarctica* caudices upon which a few larger individuals occurred (Figure 6.7 and Appendix 3, Table 3.1). Soil borne mature (≥ 3 m tall) *Olearia argophylla* possibly represent those individuals that regenerated after the last major disturbance. The long life of *Olearia argophylla* (Mueck *et al.* 1996) and its coppicing and layering ability (Neyland 1991) enable it to survive even catastrophic disturbances. Therefore in some circumstances, mature *Olearia argophylla* may be older than the canopy itself (Mueck *et al.* 1996).



Figure 6.7 An *Olearia argophylla* seedling (arrow) that has established on the caudex of a *D. antarctica*.

The persistence of large, over-mature *Olearia argophylla* in oldgrowth wet forest understoreys can be a function of its long life and acclimation to shaded conditions, yet germination may continue when suitable exposed microsites are available (e.g. *D. antarctica* caudices) and where seed release occurs proximate to those sites. Although there may be prolific germination of *Olearia argophylla* in oldgrowth wet forest, only limited

establishment is evident (Appendix 6, Table 6.1) due to insufficient insolation. In larger forest areas, observed seedling establishment of *Olearia argophylla* is predominantly due to canopy gap formation, through tree senescence and death or through fire.

With the succession of wet sclerophyll forest to cool temperate rainforest, the death of emergent Eucalypts will form gaps in which *Olearia argophylla* may establish. However, after the last eucalypts die, the incidence of gap formation in a young rainforest is very limited, thereby restricting, even further, the potential for *Olearia argophylla* establishment. It may be hundreds of years before the rainforest dominants start to die, forming gaps suitable for limited *Olearia argophylla* establishment. The radiocarbon ages obtained by Mueck, Ough and Banks (1996) suggest a maximum *Olearia argophylla* life span of 190 years (although this estimate was from only two individuals), well short of the estimated several hundred year age of *Nothofagus cunninghamii* and possibly *Atherosperma moschatum*. Consequently *Olearia argophylla* cannot persist in large areas of undisturbed rainforest unless there is a persistent seed source, such as from adjacent wet sclerophyll forest and some form of canopy disturbance (Neyland 1991). In north-eastern Tasmanian rainforest, *Olearia argophylla* may be more prevalent where small rainforest fragments exist and anthropogenic activities such as logging and burning have lead to recent disturbances.

The incidence of trees exceeding 3 m in height in the sample sites

The forest soil was the most commonly observed substrate for mature (≥ 3 m tall) *Atherosperma moschatum*, *Nothofagus cunninghamii* and *Olearia argophylla* (Appendix 3 Table 3.1). However, this may be misleading. Elevated substrates (e.g. erect *D. antarctica* caudices, fallen *D. antarctica* caudices, and coarse woody debris) can become enveloped by the trees they host (Figure 6.8). Their decay may leaving no trace, with the likelihood of this occurring increasing with time and with the size of the colonising tree. Therefore although some of the upper canopy trees may have germinated on an elevated substrate,

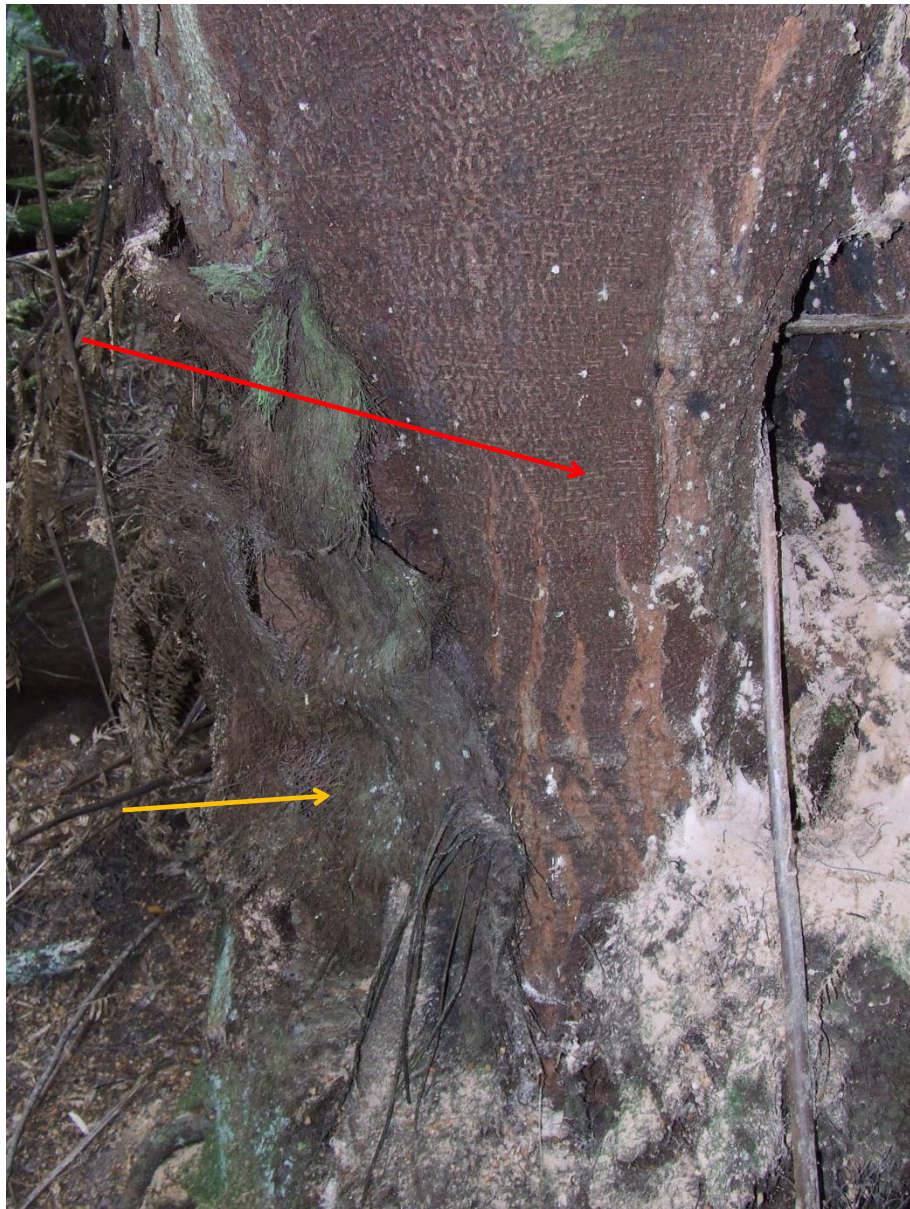


Figure 6.8 A large *Nothofagus cunninghamii* trunk (arrow) surrounded by the remnants of its ruptured *D. antarctica* host (arrow).

subsequent decay and disappearance may leave soil as the tree's apparent germination substrate.

The same may be true for mature (≥ 3 m tall) *Pittosporum bicolor* and *Tasmannia lanceolata* which were more frequently rooted in both soil and *D. antarctica* caudices compared to the other potential substrates (Appendix 3 Table 3.1). For instance the soil rooted mature (≥ 3 m tall) *Pittosporum bicolor* and *Tasmannia lanceolata* may have germinated on coarse woody debris (CWD) or fallen *D. antarctica* caudices, which has

since decayed. There is also the possibility that the dominance of forest soil as the observed substrate for mature (≥ 3 m tall) *Atherosperma moschatum*, *Nothofagus cunninghamii* and *Olearia argophylla* (Appendix 3 Table 3.1) indicates that a catastrophic or large disturbance removed the overstorey thereby increasing the sunlight available to germinates and enabling rapid growth and establishment on the exposed soil bed. Both *Atherosperma moschatum* and *Nothofagus cunninghamii* can regenerate prolifically when the overstorey is cleared by fire or logging (Neyland 1991). *Olearia argophylla* also regenerates prolifically by seed when fire exposes a suitable substrate (Ough and Ross 1992).

Height difference between size classes of each species

Frequencies of established *Atherosperma moschatum*, *Pittosporum bicolor* and *Tasmannia lanceolata* on the caudex are maximised within a height range of 0.8 m to 2.4 m on the caudex (Figure 6.1). Established *Coprosma quadrifida*, *Nothofagus cunninghamii* and *Olearia argophylla* on the tree fern caudex are most frequently found within the height range from the forest floor of 1.2 – 2.0 m, 1.2 – 2.0 m and 0 - 1.2 m respectively (Figure 6.1).

The sections of caudex where seed has been deposited and germination conditions are favourable are revealed, in part, by the histograms in Figure 6.1 which show the vertical distribution of facultative epiphyte seedlings (< 0.20 m tall) on *D. antarctica* caudices. For instance the skewed distributions of seedling (< 0.20 m tall) *Coprosma quadrifida*, *Olearia argophylla* and *Nothofagus cunninghamii*, may indicate the greater concentration of these species' seed within the height range from the forest floor of 1.2 – 2.0 m, 1.2 – 2.0 m and 0 - 1.2 m respectively (Figure 6.1). In contrast *Atherosperma moschatum* and *Pittosporum bicolor* seedlings (< 0.20 m tall) indicate a flatter more uniform distribution although still skewed towards the base of the caudex (Figure 6.1). Their distributions (Figure 6.1) suggest *Atherosperma moschatum* and *Pittosporum bicolor* are able to germinate on the caudex in greater numbers and over an increased height range than indicated for *Coprosma quadrifida*, *Olearia argophylla* and *Nothofagus cunninghamii*. *Tasmannia lanceolata*

seedlings (< 0.20 m tall) on the other hand show a centralised distribution suggesting it is unable to germinate and/or establish lower on the caudex (Figure 6.1), possibly due to an unfavourable microclimate or perhaps due to greater seed predation closer to the ground.

All established/mature (≥ 0.20 m tall) facultative epiphytes occurred on tree fern caudices at greater heights from the ground than did seedlings (< 0.20 m tall) of the same species (Table 6.6). The vertical distribution profiles (Figure 6.1) demonstrate this segregation of height differences on *D. antarctica* caudices. Dominant influences have been suggested for the caudex attachment height differences observed among epiphytic size classes (seedling < 0.20 m tall versus established/mature ≥ 0.20 m tall) of the same species, e.g. browsing from the ground, however multiple variables are most likely interacting to influence the heights of epiphyte establishment on the caudex. Increased irradiance higher on the caudex as well as added protection from terrestrial animal browsers could benefit *Atherosperma moschatum* even with its relatively high shade tolerance.

Added germination height on the *D. antarctica* caudex does not just confer advantages. Disadvantage can also arise with seedling establishment at increased height from the ground. Since caudex diameter usually decreases with height above ground, the immediately available rooting volume and potential nutrient reservoir within reach of a facultative epiphyte seedling will also diminish with height. Also since facultative epiphytes are initially more remote from the soil with increasing height on the *D. antarctica* caudex, a facultative epiphyte will take longer to root in the soil and to become nutritionally independent of the tree fern, thereby potentially suppressing its growth rate for longer. Facultative epiphyte seedlings close to the apex of the caudex are also under danger of becoming smothered by the debris ring and the fern's curtain of residual fronds, the dead and senescent fronds that are still retained and hang down from the apex of the tree fern.

Insolation

A weak positive correlation exists between the frequency of facultative epiphytes on the *D. antarctica* caudex and the variables such as crown area index (CAI), frond frequency, and residual frond frequency (Appendix 4, Table 4.1). Such a relationship may be indirect as there are strong positive correlations between crown area index (CAI), frond frequency and *D. antarctica* erect caudex length, *D. antarctica* maximum diameter and *D. antarctica* rough textured caudex length (Chapter 4). The caudex variables are in turn strongly correlated with the frequency of each of the facultative epiphyte species on the caudex (Appendix 4, Table 4.1). *Dicksonia antarctica* caudices (≥ 3 m tall) were also shown to host significantly greater frequencies of established *Atherosperma moschatum*, *Nothofagus cunninghamii*, *Pittosporum bicolor*, *Tasmannia lanceolata*, than shorter *D. antarctica* caudices (Appendix 5, Table 5.1). Therefore it appears that direct shading by the fronds of the tree fern is not as restrictive to epiphyte frequency on the caudex as is the presence of a suitable rooting medium conferred by the caudex. An analogous situation has been investigated by Gaxiola *et al.* (2008) who established that an increase in sunlight achieved by removing the fronds of *D. squarrosa* did not increase the growth of epiphyte seedlings rooted in the caudex, while the observed growth rate of seedlings rooted in soil at the base of the caudex did increase. Gaxiola *et al.* (2008) suggested that nutrient limitation restricted the growth of facultative epiphyte seedlings on *D. squarrosa* and not reduced sunlight.

Conclusion

Large *D. antarctica* caudices provided a regeneration substrate for at least 28 species of facultative epiphyte in the closed canopy wet forests of north-east Tasmania and are hence important facilitators of biodiversity. The total facultative epiphyte diversity may be larger than identified here because epiphytism varies geographically (Moffett 2000). Accordingly added diversity of *D. antarctica* facultative epiphytes may exist if the tree fern's entire range is taken into account. *Atherosperma moschatum*, *Coprosma quadrifida*, *Nothofagus cunninghamii*, *Olearia argophylla*, *Pittosporum bicolor* and *Tasmannia lanceolata* were identified as the common facultative epiphytes of *D. antarctica* caudices.

Dicksonia antarctica caudices weren't identified as the dominant germination substrate for any of the common facultative epiphyte species although they were identified as the dominant establishment substrate for *Atherosperma moschatum*, *Pittosporum bicolor* and *Tasmannia lanceolata*. Browsing and death of *Atherosperma moschatum*, *Pittosporum bicolor* and possibly *Tasmannia lanceolata* germinating on lower substrates are considered to be the cause.

The low browsing index of *Nothofagus cunninghamii* enables the species to establish on any of the four substrates regardless of height above ground, provided there is sufficient insolation, but *D. antarctica* caudices are not the dominant substrate. *Olearia argophylla* establishment on *D. antarctica* caudices is infrequent, but enables the species to persist in young rainforest. *Coprosma quadrifida* germination and establishment are predominantly in the forest soil, but still occur on *D. antarctica* caudices.

The frequencies and growth rates of all the larger species of common facultative epiphyte are potentially suppressed by the nutritional constraints of the *D. antarctica* caudex, even though there can be the addition of nutrients to the caudex through the concentration of water and litter in the apical debris ring.

When tree fern population density is high it is likely *D. antarctica* itself consumes a significant proportion of the nutrient pool. If it is nutrition which limits the growth rate and frequency of facultative epiphytes on *D. antarctica* caudices, increases in sunlight reaching the caudex will not result in substantial increases in facultative epiphyte frequency or growth rate. Although surface soil appears to be a dominant substrate for mature (≥ 3 m tall) facultative epiphyte species this may be an artefact due to the inability to determine the original germination substrate of large and old individuals.

Chapter 7: Invasion of *Dicksonia antarctica*, by apogeotropic roots of *Atherosperma moschatum*

Introduction

Apogeotropic roots grow out of the soil and up tree stems. Sanford (1987) postulated that apogeotropic roots evolved in environments with low soil nutrient availability but where a reliable source of nutrients was available via stemflow. Apogeotropic roots are thus understood to confer an advantage by providing early access to nutrients before they enter the soil and become either available to the roots of other species or unavailable due to leaching and strong absorption on soil particles and mineral complexes (Sanford 1987). It has also been proposed by Reddell *et al.* (1996), in their study of a North Queensland lowland tropical rainforest that apogeotropic roots could provide a mechanism for root respiration during periods of inundation, as well as providing early access to nutrients. Sanford (1987) did not research the possibility of a root respiration function of apogeotropic roots as his study covered *tierra firme* (non-flooded) rainforest.

The nutrients contained in stemflow are sourced from precipitation, leached vegetation and trapped litter whose type and amount will vary with geographic location and canopy composition (Herwitz 1991, Levia and Frost 2006, Zimmermann *et al.* 2007). The presence of foreign apogeotropic roots on a host may deprive the host of stemflow nutrients that would otherwise be absorbed by their own roots. There is a tendency for nutrients to be leached out of wet forest soils due to high precipitation, which suggests soil borne roots may be unable to access some of the nutrients before they are transported or leached away. Therefore uptake of nutrients from stemflow on one tree by the apogeotropic roots of a competitor means the nutrients are not lost from the community and may even again become available to the host stem as litter decomposes. A similar explanation was suggested by Turner *et al.* (2007) where stemflow nutrients taken up by epiphytes are eventually released when epiphyte litter within the host's reach decomposes, to the ultimate

benefit of the host. This highlights the possible importance of apogeotropic roots and epiphytes in maintaining nutrients within rainforest communities. There is also the possibility however that if apogeotropic roots manage to proliferate in their hosts' epiphyte mats and litter accumulations, they may be able to dominate those nutrient sources to the detriment of the host stem.

Published research on apogeotropic roots (Reddell *et al.* 1996, Sanford 1987) has focused on tropical rainforests. There has been no published literature on the phenomenon in temperate forests other than Ashton's (2000) observation of the presence of terrestrially sourced *Atherosperma moschatum* roots in the root mantle of *D. antarctica*. Tree ferns with a thick root mantle are a likely substrate for apogeotropic roots of other species, *Dicksonia antarctica* especially since it possesses an erect rhizome that is encompassed by a thick mantle of fibrous roots, achieving a diameter up to two metres at its base. The *D. antarctica* root mantle is permeable, has a high moisture holding capacity (Roberts *et al.* 2005) and provides for a continuous substrate stretching from the soil up the caudex to several metres above ground, depending on the size of the fern. The root mantle provides an ideal substrate for plants and a wide range of obligate and facultative epiphytes will germinate and grow on it (previous chapters, also (Chaffey 1999, Duncan and Isaac 1994, Garrett 1996b, Wapstra *et al.* 2003)). The ability of some facultative epiphyte species to extend their root systems down through the root mantle and into the soil suggests that tree roots can also grow from the ground up through the root mantle.

This chapter reports observations of the origin of apogeotropic roots growing in the root mantle of *D. antarctica* in the sample field sites of north-eastern Tasmania. Since apogeotropic roots in other situations (Reddell *et al.* 1996, Sanford 1987) have been linked to the benefit of nutrient uptake from stemflow, this proposed function is of particular interest in the present investigation. Harvesting of the nutrient resource in the *D. antarctica* root mantle by apogeotropic roots of invading species may in turn deprive the tree fern of resource supply. This poses the question: Are host *D. antarctica* detrimentally affected by

the presence of those roots? To investigate this question the current chapter tests the hypothesis that:

- *Dicksonia antarctica* specimens invaded by apogeotropic roots have greater mortality and morbidity, than non-invaded *D. antarctica*.

Frond size is critical to catchment size of the rosette of *D. antarctica* (which captures water and nutrients), and to debris ring integrity. Therefore it is hypothesized that:

- *Dicksonia antarctica* invaded by apogeotropic roots will have a smaller length of the caudex covered by the debris ring (length of debris ring) compared to non-invaded *D. antarctica*.

Reddell, Hopkin and Graham (1996) and Sanford (1987) indicate an association of the apogeotropic root phenomena with low soil nutrient availability. A similar trigger could occur in temperate wet forests. A site's geology, climate, slope, aspect, and topography will contribute to influence soil fertility. The degree of competition among plant species present will also impact on apparent soil fertility via resource accessibility by individuals. The present chapter investigates these influences by testing the following hypotheses:

- The density of invaded *D. antarctica* caudices will be greater on sites of inferred low soil fertility compared to the density on sites of inferred high fertility;
- The density of invaded *D. antarctica* caudices will be greater on sites comprising topographic features that minimise soil depth compared to the density on sites comprising topographic features that maximise soil depth (relatively speaking);
- The density of invaded *D. antarctica* caudices is positively correlated with rainfall (mean annual rainfall);
- The density of invaded *D. antarctica* caudices is positively correlated with the density of canopy/subcanopy stems (all species);
- The density of invaded *D. antarctica* caudices is positively correlated with the density of *Atherosperma moschatum* canopy/subcanopy stems; and

- The density of invaded *D. antarctica* caudices is positively correlated with degrees of slope.

The likelihood of tree roots intercepting and invading the *D. antarctica* caudex will be influenced by the densities of both the tree fern caudices and the apogeotropic root sources. The present chapter investigates these influences by testing the hypotheses that:

- The density of *D. antarctica* caudices invaded by apogeotropic roots increases with the density of dominant (canopy and subcanopy) *Atherosperma moschatum* stems, and increases with the density of *D. antarctica* caudices.

The larger *D. antarctica* caudices are typically the older specimens and hence apogeotropic roots should have had more time to invade their caudex compared to smaller specimens of *D. antarctica*. This explanation will be analysed by testing the following hypothesis:

- Larger *D. antarctica* caudices are more likely to be invaded by apogeotropic roots than smaller *D. antarctica* caudices.

Combinations of the above variables may act to influence the density of *D. antarctica* caudices, either invaded or not by apogeotropic roots. Consequently appropriate selections of the above variables will be tested to determine the combination (if any) with the greatest influence on the density of *D. antarctica* caudices found to be invaded by apogeotropic roots.

Analysis

The 19 field sample plots described in Chapter 3 (Site Selection and Field Sampling) provided the database for this analysis of morphological, apogeotropic and site variables associated with *D. antarctica* in north-east Tasmania. A glossary of abbreviations appears on page 9 of this thesis.

The Chi-Square Test (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- Larger *D. antarctica* caudices are more likely to be invaded by apogeotropic roots than smaller *D. antarctica* caudices.

The Chi-Square Test identifies whether the six *D. antarctica* size classes (≤ 1.0 m, > 1.0 to ≤ 2.0 m, > 2.0 to ≤ 3.0 m, > 3.0 to ≤ 4.0 m, > 4.0 to ≤ 5.0 m, and > 5.0 m) and the two invasion classes (non-invaded and invaded) are either independent or associated.

Several hypotheses were tested by identifying which classes of site factors (fertility, topography and aspect) were associated with the density of invaded *D. antarctica* caudices. Individual ANOVAs (α 0.05) (MINITAB 2005) were used to determine the association. Likewise, the individual correlations of the density of invaded *D. antarctica* caudices with the continuous site variables of rainfall, slope, elevation, density of canopy and subcanopy *Atherosperma moschatum* stems, density of canopy and subcanopy stems (all species), and density of all *D. antarctica* caudices were analysed using the Pearson correlation (α 0.05) (MINITAB 2005). For those class variables found to be in association with the density of invaded *D. antarctica* caudices, the ANOVA (α 0.05) (MINITAB 2005) was repeated, but with the addition of a covariate to the model. The covariate was selected as the continuous variable identified as being correlated with the density of invaded *D. antarctica* caudices.

The hypotheses tested were as follows:

- The density of invaded *D. antarctica* caudices will be greater on sites of apparent low fertility compared to the density on sites of apparent high fertility;
- The density of invaded *D. antarctica* caudices will be greater on sites comprising topographic features that minimise soil depth compared to the density on sites comprising topographic features that maximise soil depth (relatively speaking);
- The density of invaded *D. antarctica* caudices is positively correlated with rainfall;
- The density of invaded *D. antarctica* caudices is positively correlated with the density of canopy/subcanopy stems (all species);
- The density of invaded *D. antarctica* caudices is positively correlated with the density of *Atherosperma moschatum* canopy/subcanopy stems; and

- The density of invaded *D. antarctica* caudices is positively correlated with degrees of slope.

The hypothesis that *Dicksonia antarctica* specimens invaded by apogeotropic roots have greater mortality and morbidity, than non-invaded *D. antarctica* was tested by first identifying the relationship between fronds and erect stem length of non-invaded *D. antarctica*. This was achieved by using the fitted line plot option in MINITAB (2005) to separately regress (α 0.05) the erect stem length of non-invaded *D. antarctica* with frond length, lamina maximum width, lamina length, frond area index, and frond frequency respectively. The use of the fitted line plot option in MINITAB (2005) enabled the relationship between the response variable and the predictor to be identified as either linear, quadratic, or cubic. The equations of the regression relationships identified as significant were used to predict the frond length, lamina maximum width, lamina length, and frond frequency of *D. antarctica* invaded by apogeotropic *Atherosperma moschatum* roots. Separate ANOVAs (α 0.05) (MINITAB 2005) were then used to determine if significant variation was present between the predicted and actual frond length, lamina maximum width, lamina length, frond area index, and frond frequency of invaded *D. antarctica* respectively with *D. antarctica* size class selected as a random factor.

The Kruskal-Wallis Test (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- *Dicksonia antarctica* invaded by apogeotropic roots will have a smaller length of the caudex covered by the debris ring (debris ring length) compared to non-invaded *D. antarctica*.

In this test debris ring length is the response variable and caudex invasion class is the factor.

The Chi-Square Test (α 0.05) (MINITAB 2005) was used to test the hypothesis that:

- *Dicksonia antarctica* specimens invaded by apogeotropic roots have greater mortality and morbidity, than non-invaded *D. antarctica*.

The Chi-Square Test identified whether the two *D. antarctica* health classes (alive and dead) and the three invasion classes (no apogeotropic roots visible, 1 to ≤ 4 apogeotropic roots visible around the exterior circumference of the root mantle, and > 4 apogeotropic roots visible around the exterior circumference of the root mantle) were either independent or associated.

Results

Apogeotropic roots of one or more of four woody angiosperm species *Atherosperma moschatum*, *Nothofagus cunninghamii*, *Olearia argophylla*, and *Acacia melanoxylon*, were present in the root mantle of some erect *D. antarctica* caudices (Table 7.1). The rhizomes of three typically terrestrial pteridophytes *Histiopteris incisa*, *Hypolepis rugulosa* and *Pteridium esculentum* were also observed in the root mantle of erect *D. antarctica* caudices, but whether these had grown into the root mantle from the forest substrate or vis-a-versa could not be determined.

The overwhelming majority of apogeotropic roots which were observed to invade *D. antarctica* caudices belonged to the tree species *Atherosperma moschatum* (Table 7.1 and Figure 7.1). Consequently the investigation of the apogeotropic phenomenon is focused on the invasion of the *D. antarctica* caudex by this common rainforest tree species. The absolute maximum height of apogeotropic roots observed in a *D. antarctica* caudex was 6.5 m above ground (*Atherosperma moschatum*, Table 7.2). Note, these observations were based on external assessment of the *D. antarctica* caudex and therefore the apogeotropic roots may possibly have exceeded the recorded height extension internally but were obscured by the tree fern caudex itself. The absolute frequency of invaded *D. antarctica* caudices increases from *D. antarctica* caudex length classes 1 to 4, then decreases in classes 5 and 6 (Figure 7.2). The percentage of the total *D. antarctica* caudices, which are invaded by apogeotropic *Atherosperma moschatum* roots, progressively increases with *D. antarctica* caudex length, from size class 1 to class 6 (Figure 7.3).

Table 7.1 Frequency of *D. antarctica* caudices invaded by apogeotropic roots per site. Table includes total frequency of invaded *D. antarctica* caudices (some caudices have been invaded by the apogeotropic roots of more than one species), the frequency of *D. antarctica* caudices invaded by apogeotropic roots of each of the following species *Atherosperma moschatum*, *Nothofagus cunninghamii*, *Olearia argophylla*, *Acacia melanoxylon* and the frequency of *D. antarctica* caudices invaded by rhizomes of *Histiopteris incisa* and *Hypolepis rugulosa*, which may have originated from the forest substrate.

Site	Frequency of <i>D. antarctica</i> caudices invaded by apogeotropic roots							<i>D. antarctica</i> caudex frequency
	Total	<i>Atherosperma moschatum</i>	<i>N. cunninghamii</i>	<i>O. argophylla</i>	<i>Acacia melanoxylon</i>	<i>Histiopteris incisa</i>	<i>Hypolepis rugulosa</i>	
1	2	2	0	0	0	0	0	36
2	1	1	0	0	0	0	0	14
3	17	15	3	0	0	1	0	52
4	14	14	0	0	0	0	0	69
5	34	34	3	0	0	0	0	75
6	5	4	0	1	0	0	0	53
7	3	0	0	0	0	0	3	43
8	5	3	2	0	0	0	0	30
9	12	12	2	0	0	0	0	62
10	40	40	0	0	0	1	0	62
11	0	0	0	0	0	0	0	50
12	25	25	1	0	0	0	0	77
13	6	6	0	0	0	0	0	46
14	1	0	1	0	0	0	0	69
15	0	0	0	0	0	0	0	52
16	1	1	0	0	0	0	0	60
17	9	7	2	0	1	0	0	93
18	1	0	0	0	0	1	0	81
19	1	0	1	0	0	0	0	43

Table 7.2 Mean maximum height apogeotropic roots were observed on *D. antarctica* caudices for each site, the highest maximum height apogeotropic roots were observed on a *D. antarctica* stem for each site, the mean maximum apogeotropic root diameter observed on *D. antarctica* caudices for each site, and the greatest maximum apogeotropic root diameter observed on *D. antarctica* caudices for each site. Am, *Atherosperma moschatum*; Nc, *Nothofagus cunninghamii*; Oa, *Olearia argophylla*; Ac, *Acacia melanoxylon*.

Site	Mean height (m)				Maximum height (m)				Mean maximum root diameter (mm)				Greatest maximum root diameter (mm)			
	Am	Nc	Oa	Ac	Am	Nc	Oa	Ac	Am	Nc	Oa	Ac	Am	Nc	Oa	Ac
1	1.45	-	-	-	2.30	-	-	-	18	-	-	-	18	-	-	-
2	2.10	-	-	-	2.10	-	-	-	10	-	-	-	10	-	-	-
3	1.32	0.09	-	-	3.20	0.15	-	-	46	20	-	-	200	20	-	-
4	2.52	-	-	-	6.50	-	-	-	89	-	-	-	450	-	-	-
5	1.89	2.28	-	-	4.90	4.90	-	-	42	120	-	-	190	230	-	-
6	1.28	-	0.16	-	2.91	-	0.16	-	16	-	30	-	25	-	30	-
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	1.39	1.4	-	-	1.80	1.5	-	-	12	9	-	-	20	12	-	-
9	1.14	0.60	-	-	2.06	0.67	-	-	11	13	-	-	25	15	-	-
10	1.26	-	-	-	3.12	-	-	-	21	-	-	-	170	-	-	-
11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	1.46	4.0	-	-	4.00	4.0	-	-	40	14	-	-	230	14	-	-
13	1.33	-	-	-	2.02	-	-	-	19	-	-	-	80	-	-	-
14	-	1.75	-	-	-	2.43	-	-	-	228	-	-	-	400	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	0.61	-	-	-	0.61	-	-	-	1	-	-	-	1	-	-	-
17	1.10	1.43	-	0.11	1.73	2.00	-	0.11	22	14	-	110	130	20	-	110
18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	-	1.73	-	-	-	1.73	-	-	-	30	-	-	-	30	-	-



Figure 7.1 Apogeotropic *Atherosperma moschatum* roots (arrow) visible on the exterior of a *D. antarctica* caudex.

A significant association exists between *D. antarctica* size class and *D. antarctica* invasion class (Table 7.3). This means more of the smaller *D. antarctica* caudices (with length classes 1 and 2 of 6) were not invaded by *Atherosperma moschatum* roots than was to be expected by chance, whereas a greater proportion of the larger *D. antarctica* caudices (size class 4, 5 and 6) were invaded by *Atherosperma moschatum* roots than expected by chance (Table 7.3).

Significant variation was identified between the density of *D. antarctica* caudices invaded by *Atherosperma moschatum* apogeotropic roots on low site fertility (class 1) and high site fertility (class 2), with 23.9 % of variation being explained by the model, with no covariates selected (Table 7.4). Sample sites of fertility class 1 (low) have a mean density of 2.60 invaded *D. antarctica* caudices per sample plot out of a total density of 11.22 caudices per sample plot. Sample sites of fertility class 2 (high) show a mean density of 0.43 invaded *D. antarctica* caudices out of a total density of 7.43 caudices. No significant variation in the

density of *D. antarctica* caudices invaded by *Atherosperma moschatum* apogeotropic roots was identified between the two aspect classes, nor with respect to topography (Table 7.4).

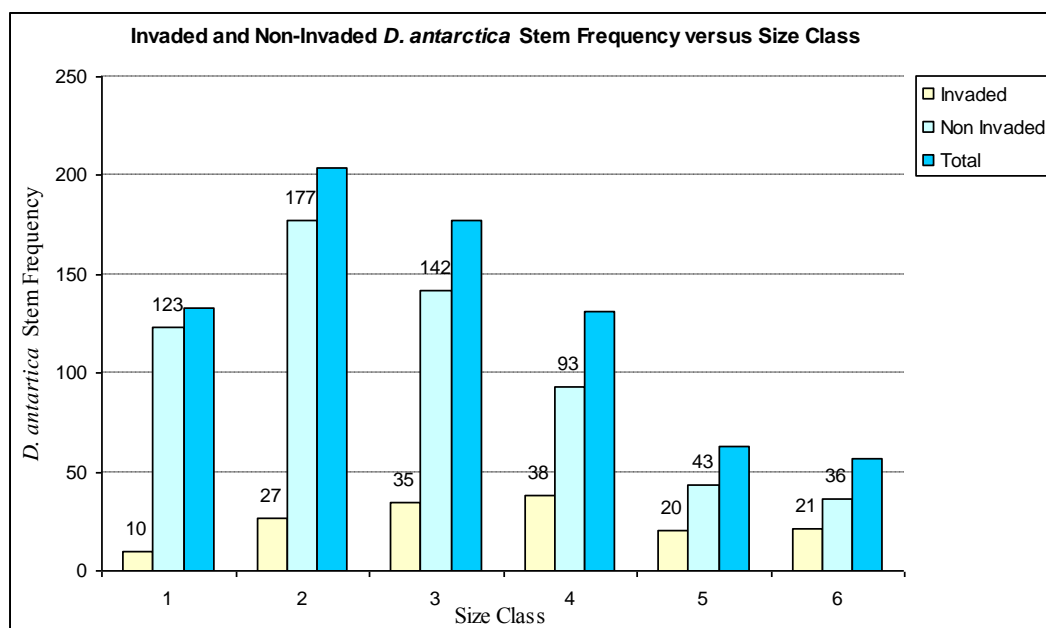


Figure 7.2 Frequency of *D. antarctica* caudices invaded and non-invaded by *Atherosperma moschatum* apogeotropic roots for each erect *D. antarctica* caudex length size class across all sample sites. Size class 1, ≤ 1.0 m; size class 2, > 1.0 to ≤ 2.0 m; size class 3, > 2.0 to ≤ 3.0 m; size class 4, > 3.0 to ≤ 4.0 m; size class 5, > 4.0 to ≤ 5.0 m; size class 6, > 5.0 m.

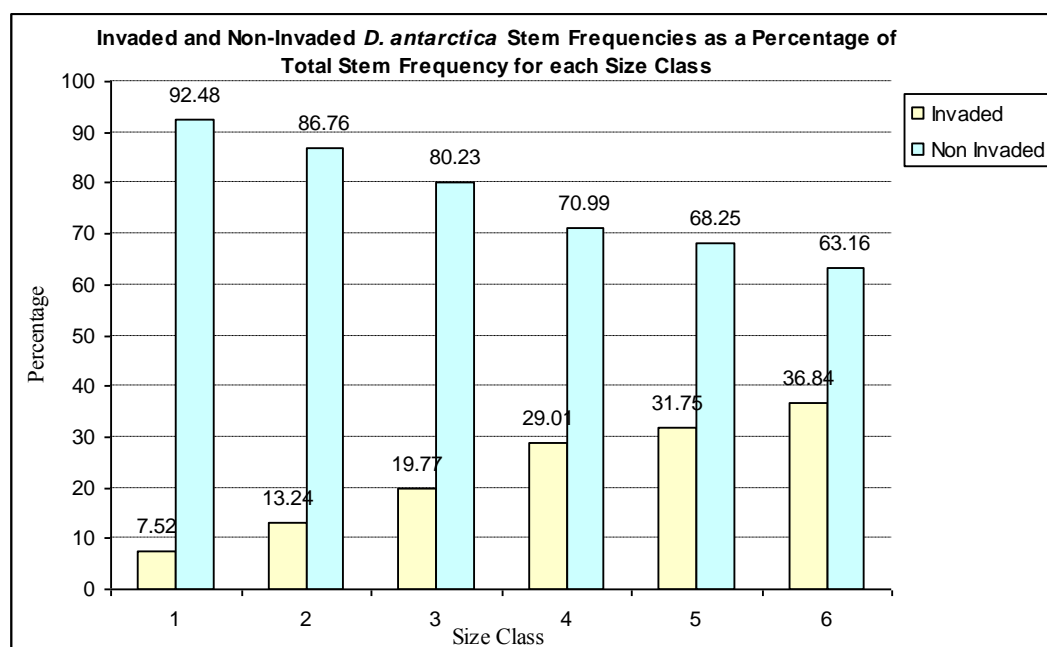


Figure 7.3 Invaded and non-invaded *D. antarctica* caudex frequencies as a percentage of total caudex frequency for each erect *D. antarctica* caudex length size class across all sample sites. Size class 1, ≤ 1.0 m; size class 2, > 1.0 to ≤ 2.0 m; size class 3, > 2.0 to ≤ 3.0 m; size class 4, > 3.0 to ≤ 4.0 m; size class 5, > 4.0 to ≤ 5.0 m; size class 6, > 5.0 m.

Table 7.3 Chi-Square Test (α 0.05) two way table of invasion class (Invasion class 0, non-invaded; invasion class 1, invaded) versus *D. antarctica* caudex length size class (Size class 1, ≤ 1.0 m; size class 2, > 1.0 to ≤ 2.0 m; size class 3, > 2.0 to ≤ 3.0 m; size class 4, > 3.0 to ≤ 4.0 m; size class 5, > 4.0 to ≤ 5.0 m; size class 6, > 5.0 m). The Pearson Chi-Square = 41.35, df = 5, $p < 0.001$. The Likelihood Ratio Chi-Square = 42.02, df = 5, $p < 0.001$.

Size Class		Invasion Class		Total
		0	1	
1	Observed count	123	10	133
	Expected count	107	26	133
	Chi-Square contributions	2	10	-
2	Observed count	177	27	204
	Expected count	164	40	204
	Chi-Square contributions	1	4	-
3	Observed count	142	35	177
	Expected count	142	35	177
	Chi-Square contributions	0	0	-
4	Observed count	93	38	131
	Expected count	105	26	131
	Chi-Square contributions	1	6	-
5	Observed count	43	20	63
	Expected count	51	12	63
	Chi-Square contributions	1	5	-
6	Observed count	36	21	57
	Expected count	46	11	57
	Chi-Square contributions	2	8	-
Total		614	151	765

Table 7.4 Separate ANOVA (α 0.05) of site fertility, topography, and aspect classes with invaded *D. antarctica* stem density as the response. No covariates. R^2 values are adjusted. (*, $p \leq 0.05$; ns, not significant). Class 1 (low) and class 2 (high).

Model	Mean		F	R^2
	Class 1	Class 2		
Fertility class	2.60	0.43	5.40*	23.92 %
Topography class	ns	ns	2.69ns	26.57 %
Aspect class	ns	ns	2.77ns	33.55 %

The Pearson correlation identified a significant positive relationship (correlation coefficient 0.749) between the density of *D. antarctica* caudices invaded by apogeotropic roots and the combined density of canopy and subcanopy *Atherosperma moschatum* stems (Table 7.5). No significant correlation was identified between the density of invaded *D. antarctica* caudices and each of the variables degrees of slope, elevation, the density of canopy and subcanopy stems (all species), and the density of *D. antarctica* caudices (invaded and non invaded) (Table 7.5).

A significant variation was identified in the density of *D. antarctica* caudices invaded by *Atherosperma moschatum* apogeotropic roots between sites with low fertility (class 1) and sites with high fertility (class 2), with 70.47% of variation being explained by the model, with the density of canopy and subcanopy *Atherosperma moschatum* stems selected as a covariate (Table 7.6). Class one (low fertility) possessed the greater mean density of invaded caudices.

Table 7.5 Separate Pearson correlations (α 0.05) of invaded *D. antarctica* caudex density versus each of the variables density of canopy and subcanopy stems (all species), density of canopy and subcanopy *Atherosperma moschatum* stems, density of *D. antarctica* caudices, slope, elevation, and mean annual rainfall. (***, $p \leq 0.001$; ns, not significant).

Variable	Pearson correlation
Density of canopy and subcanopy <i>Atherosperma moschatum</i> stems	0.749***
Density of canopy and subcanopy stems (all species)	-0.178ns
Density of <i>D. antarctica</i> caudices	0.448ns
Slope	-0.159ns
Elevation	0.072ns
Rainfall	0.170ns

Table 7.6 ANOVA (α 0.05) of invaded *D. antarctica* stem density between fertility classes. Dominant (subcanopy and canopy) *Atherosperma moschatum* (A.m) stem density has been selected as a covariate. Class 1 (low) and class 2 (high). (***, $p \leq 0.001$; *, $p \leq 0.05$)

Response	Model Components		F	R-Sq(adj)	Class with greater mean
	Type	Variable			
Invaded caudex density	Covariate	<u>A.m</u> canopy & subcanopy density	21.49***	70.47%	na
	Factor	Site fertility	8.84*		1*

Separate significant positive relationships were identified between *D. antarctica* erect caudex length and the frond variables of non-invaded *D. antarctica* as follows: frond length, lamina length, lamina width, frond area index, and frond frequency. The regression equations, r^2 values, F values and p values, for each of the regressed variables, versus *D. antarctica* erect caudex length are listed in Table 7.7. The fitted line plots for each regression are displayed in Figure 7.4.

Table 7.7 Results of regressions of live frond frequency, frond length, lamina length, lamina width, and frond area index, respectively, versus erect stem length of non-invaded *D. antarctica*, where y = frond variable, and x = erect stem length. (***, $p \leq 0.001$; **, $p \leq 0.01$).

Characteristic (y)	Regression Equation	R ² (adj)	ANOVA (F)
Frond Frequency	$y = 0.1051 + 0.6694x - 0.1013x^2$	42.5%***	18.57**
Frond Length	$y = 0.1096 + 0.6213x - 0.1383x^2$	35.8%***	23.89**
Lamina Length	$y = 0.1254 + 0.6453x - 0.1197x^2$	38.0%***	18.58**
Lamina Width	$y = 0.7222 + 0.09469x - 0.04154x^2$	23.8%***	44.58**
Frond Area Index	$y = 0.1383 + 0.5944x - 0.1605x^2$	36.0%***	34.65**

Significant variation was identified between those values predicted by the non-invaded *D. antarctica* regression equations and those values actually recorded from invaded *D. antarctica* with size class selected as a random factor (Table 7.8). The actual mean was significantly lower than the predicted mean for frond frequency, frond length, lamina length, lamina width, and frond area index (FAI) (Table 7.8).

Significant variation was identified in debris ring length among the two invasion intensity classes. *Dicksonia antarctica* invaded by apogeotropic roots showed a significantly smaller debris ring length (median 0.12 m) compared with non-invaded *D. antarctica* caudices (median 0.16 m) (Table 7.9).

A significant association was identified between *D. antarctica* health class (health class 0, dead; health class 1, alive) and *D. antarctica* caudex invasion intensity class (invasion intensity class 0, no apogeotropic roots visible; invasion intensity class 1, 1 to ≤ 4 apogeotropic roots visible around the exterior circumference of the root mantle; invasion intensity class 2, > 4 apogeotropic roots visible around the exterior circumference of the root mantle). The observed count of dead *D. antarctica* caudices was less than expected for invasion intensity class 0, but was greater than expected for invasion intensity classes 1, and 2 (Table 7.10).

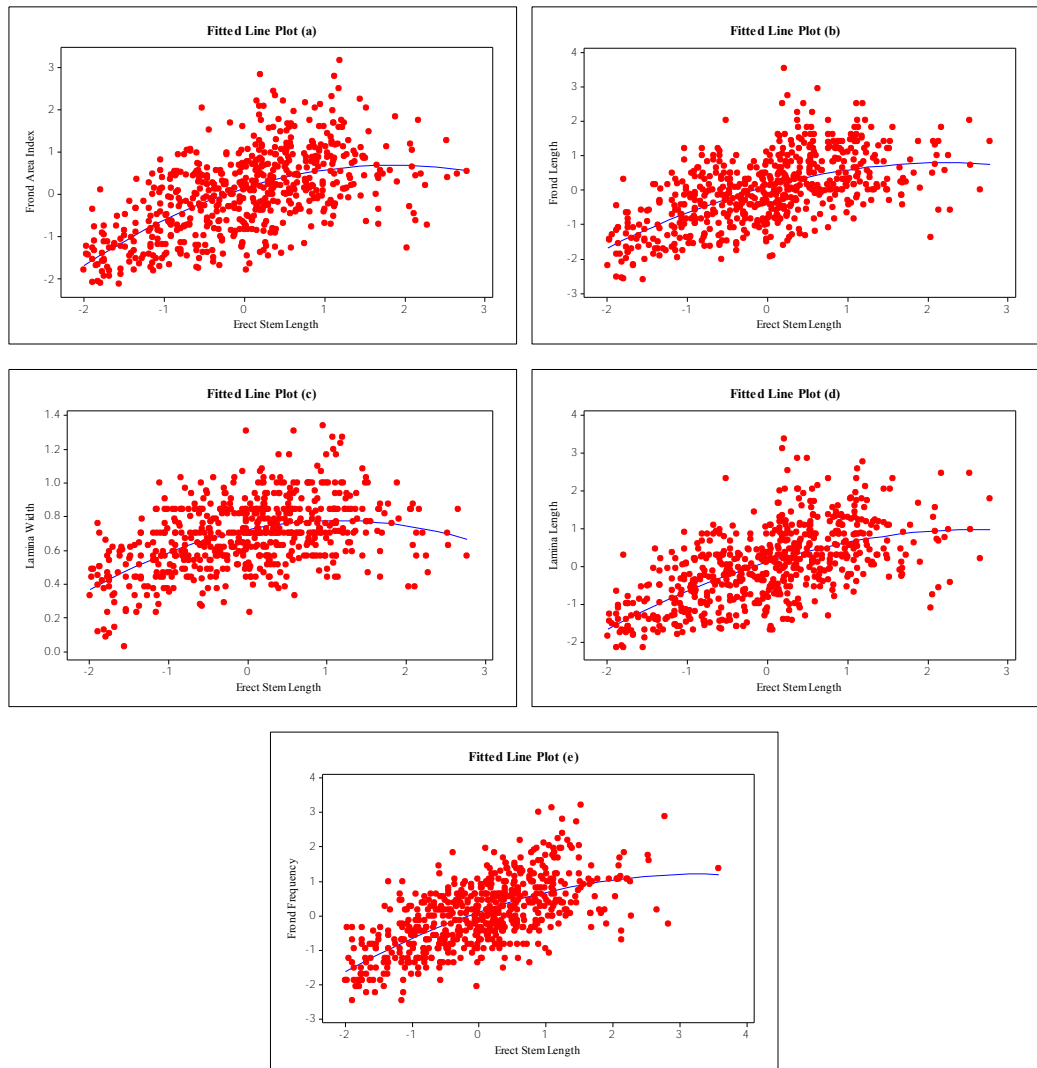


Figure 7.4 Regression fitted line plots of (a) *D. antarctica* frond area index (y) versus *D. antarctica* erect stem length (x). (b) *D. antarctica* frond length (y) versus *D. antarctica* erect stem length (x). (c) *D. antarctica* lamina width (y) versus *D. antarctica* erect stem length (x). (d) *D. antarctica* lamina length (y) versus *D. antarctica* erect stem length (x). (e) *D. antarctica* frond frequency (y) versus *D. antarctica* erect stem length (x). Both the x and y variables are transformed to meet the assumptions of the test.

Table 7.8 Results of five, ANOVA (α 0.05) comparing predicted frond size and frequency values of invaded *D. antarctica* obtained from the regression equations identified by Test 5, and the actual frond size and frequency values recorded from the field. *D. antarctica* erect caudex size class (6 classes) has been included as a random variable. The predicted and actual values are for the following variables: frond frequency, frond length, lamina length, lamina width, and frond area index. The percentage difference between the actual and predicted values is also displayed. (***, $p \leq 0.001$).

Frond Variable	Model	F	Mean		Actual difference from predicted %
			Actual	Predicted	
Frond frequency	Actual/Predicted	31.17***	18.42	22.52	- 18.21 %
	Size Class	15.48***			
Frond length (m)	Actual/Predicted	17.27***	2.59	2.87	- 9.76 %
	Size Class	13.99***			
Lamina length (m)	Actual/Predicted	11.37***	2.24	2.51	- 10.76 %
	Size Class	14.97***			
Lamina width (m)	Actual/Predicted	25.53***	0.76	0.83	- 8.43 %
	Size Class	8.84***			
Frond area index (m ²)	Actual/Predicted	17.30***	0.89	1.02	- 15.66 %
	Size Class	13.17***			

Table 7.9 Kruskal-Wallis Test (α 0.05) of *D. antarctica* caudex debris ring length between invasion classes (Invasion class 0, non-invaded; invasion class 1, invaded). (adjusted for ties).

Invasion Intensity Class	N	Median	Ave Rank	Result
0	606	0.16	387.0	H = 6.71 df = 1 p = 0.010
1	147	0.12	335.7	

Table 7.10 Chi-Square Test (α 0.05) two way table of *D. antarctica* invasion intensity class (Invasion intensity class 0, no apogeotropic roots visible; invasion intensity class 1, 1 to \leq 4 apogeotropic roots visible around the exterior circumference of the root mantle; invasion intensity class 2, $>$ 4 apogeotropic roots visible around the exterior circumference of the root mantle) versus health class (health class 0, dead; health class 1, alive). Chi-Sq = 7.79, df = 2, p = 0.02.

Invasion Intensity Class		Health Class		Total
		0 (Dead)	1 (Alive)	
0	Observed count	20	611	631
	Expected count	26.23	604.77	
	Chi-Square contributions	1.4778	0.0641	
1	Observed count	7	105	112
	Expected count	4.65	107.35	
	Chi-Square contributions	1.1814	0.0512	
2	Observed count	6	45	51
	Expected count	2.12	48.88	
	Chi-Square contributions	7.1036	0.3080	
Total		33	761	794

Discussion

Atherosperma moschatum is by far the most frequent species whose apogeotropic roots were observed to invade *D. antarctica* caudices (Table 7.1 and Figure 7.5). *Acacia melanoxylon*, *Nothofagus cunninghamii* and *Olearia argophylla* were the other species whose apogeotropic roots were observed in the caudex of *D. antarctica*. *Atherosperma moschatum* also produces a prolific amount of adventitious roots that extend throughout the top-soil and litter. Such roots in other species tend to proliferate in microsites of enriched nutrient concentrations (e.g. litter, faeces, stemflow drip points) in order to maximise nutrient uptake (de Kroon and Mommer 2006). If *D. antarctica* caudices contain a favourable nutrient or water source then apogeotropic *Atherosperma moschatum* roots may be favoured to grow into the *D. antarctica* caudex when adventitious *Atherosperma moschatum* roots intercept a zone of enhanced nutrient availability at the base of a tree fern. Hence the observed pervasiveness of adventitious *Atherosperma moschatum* roots could

lead to the observed frequency of apogeotropic *Atherosperma moschatum* roots in *D. antarctica* caudices sampled.



Figure 7.5 Apogeotropic roots of *Atherosperma moschatum* (arrow) visible on the exterior of a *D. antarctica* caudex.

It cannot be determined from the data when *D. antarctica* caudices first become invaded with apogeotropic *Atherosperma moschatum* roots. The increased frequency of invaded *D. antarctica* caudices from size classes 1 to 4 (comprised of caudices with lengths ≤ 4.0 m) (Figure 7.2) could represent increasing invasions as *D. antarctica* caudices grow and age, which implies that invasion can occur in caudices of any size class. The pattern of additional frequency of invasion suggests that many added invasions are incurred between caudex size classes 1 and 2 (comprised of caudices with lengths ≤ 2.0 m) (Figure 7.2). The data indicate that apogeotropic roots are not attracted solely to the bigger and older *D. antarctica* stems, instead the bulk of invaded *D. antarctica* caudices are found in mid-size classes 2, 3, and 4 (comprised of caudices with lengths > 1.0 to ≤ 4.0 m). This suggests that apogeotropic roots are not attracted to *D. antarctica* caudices because of the senescence or old age of the tree fern, even allowing for the fact that tree fern senescence can occur due to

other factors besides old age, e.g. closure of a canopy gap by a dense canopy, restricting light levels.

The positive association between tree fern size class (based on caudex length) and invasion by *Atherosperma moschatum* roots indicates the larger size classes contain a greater number of invaded *D. antarctica* caudices than would be expected through chance (Figure 7.3 and Table 7.3). Although this suggests apogeotropic roots are attracted to larger and therefore older stems, from Figure 7.3 it can be seen that the percentage of *D. antarctica* caudices that are not invaded drops substantially from caudex size class 3 to class 5 whereas the invaded caudex frequency increases. Since larger *D. antarctica* caudices have a tendency to fall over due to their size, especially if they develop a tilt, the presence of apogeotropic roots in the caudex may anchor the tree fern and help it stay erect longer compared to non-invaded *D. antarctica*.

The significantly greater density of *D. antarctica* caudices invaded by apogeotropic *Atherosperma moschatum* roots (2.60 per 100 m²) on low fertility sites, compared to high fertility sites (0.43 per 100 m²) indicates a link between *Atherosperma moschatum* apogeotropic root invasion of *D. antarctica* and low soil nutrient availability. This result corresponds with that of other authors who have researched the apogeotropic root phenomenon (Reddell *et al.* 1996, Sanford 1987). Sanford (1987) linked the presence of apogeotropic roots on a host tree with the presence of nutrients in stemflow. A similar situation could exist between *D. antarctica* and *Atherosperma moschatum* in these forests. Possible evidence for the presence of a significant nutrient source atop the *D. antarctica* caudex has been explored by Dearden and Wardle (2008) who identified a species of small tree fern, *Blechnum discolor* (Forst.) Keys., as a considerable influence on nutrient distribution, through it collecting and retaining litter in its apical frond rosette. The retained litter decomposes and the released nutrients are absorbed by the roots of *Blechnum discolor* when they reach the soil.

The Dearden and Wardle (2008) study provides an example of a tree fern whose growth habit, in several ways, parallels *D. antarctica* and the study can be used as a basis to theorise that the decomposing debris ring of *D. antarctica* (when present) provides the fern with a concentrated nutrient source, which is detectable by other species' roots in the soil. The root mantle could also be a nutrient source as stemflow will leach nutrients from its roots, and microbial and invertebrate activity within the root mantle will release nutrients from enveloped litter and root mantle debris. Unfortunately, determining the level of nutrients in *D. antarctica* stemflow, the nutrient source and whether the nutrients are detected by *Atherosperma moschatum* roots in the surrounding soil, are all areas of investigation which remain outside the bounds of this study.

On drier sites the concentration of canopy litter and throughfall which is funnelled into the tree fern's apical rosette may in turn also provide a sufficient attraction to *Atherosperma moschatum* roots to induce their invasion of the caudex. However this study did not include field sample plots in forests with low rainfall simply because these did not contain large mature *D. antarctica* in sufficient densities for the analysis (Chapter 3).

Two explanations can be considered in light of the significant variation between the invasion densities of low and high fertility sites. The first scenario is that the effect of site fertility on invaded *D. antarctica* caudex density is indirect and instead a greater non-invading root biomass exists in the more fertile soils, which limits the incidence of *Atherosperma moschatum* roots intercepting *D. antarctica* caudices. Conversely the lower root biomass of low fertility sites would enable *Atherosperma moschatum* roots to intercept a greater number of tree ferns than would otherwise be the case. However, if we assume tree stem density is representative of biomass then the lack of significant correlations between invaded *D. antarctica* caudex density and dominant tree stem density, and between invaded *D. antarctica* caudex density and the combined tree stem density of the two highest tree strata negate this explanation (Table 7.5).

The second scenario assumes the level of site fertility will influence the degree to which *Atherosperma moschatum* seeks access to additional nutrient sources. On sites of low soil fertility, *Atherosperma moschatum* may invade a greater number of *D. antarctica* caudices compared to those on sites of high fertility, in order to maximise access to a more limiting nutrient supply. Assuming this, has *Atherosperma moschatum* responded to low soil fertility by increasing the degree to which it proliferates roots into nutrient rich microsites, such as the *D. antarctica* caudex, or is it foraging more widely through the soil and thereby intercepting a greater number of *D. antarctica* caudices, which it then invades, or are both mechanisms at play? Since nutrient rich patches can occur in soils of low or high fertility, and some *Atherosperma moschatum* still invade *D. antarctica* caudices in sites classed as possessing high fertility (albeit at a lower frequency), it is suggested that *Atherosperma moschatum* proliferates roots into nutrient rich microsites regardless of overall soil fertility. Therefore an increase in the distance across which *Atherosperma moschatum* roots have to forage on low fertility sites is a likely reason why invaded *D. antarctica* density is greater on sites classed as low fertility compared to those classed as high fertility. Further research is required for this explanation to be confirmed, e.g. quantitative evidence showing how *Atherosperma moschatum* responds in relation to apogeotropic invasion of *D. antarctica* in soils of varying levels of fertility.

A significant strong positive correlation was shown to exist between *Atherosperma moschatum* density and invaded *D. antarctica* caudex density (Table 7.5). Such a relationship points towards the influence which the density of *Atherosperma moschatum* stems and their roots have on the likelihood of a *D. antarctica* caudex being encountered and invaded by those roots. Although *D. antarctica* caudex density could be expected to show a similar relationship, in fact no significant correlation was identified (Table 7.5). A reason for this discrepancy could be that not all *D. antarctica* caudices provide the appropriate conditions that will result in invasion by apogeotropic *Atherosperma moschatum* roots. The size and make-up of a tree fern's debris ring and root mantle, as well as their invertebrate fauna and associated decomposition will influence the type and amount

of nutrients available to invading apogeotropic *Atherosperma moschatum* roots. Likewise, the nutritional and growth status of *Atherosperma moschatum* and availability of nutrient supply from conventional (non-invasive) means may influence this outcome in the vicinity of individual trees.

Both the frond frequency and frond size of non-invaded *D. antarctica* caudices vary with erect stem length (Table 7.7 and Figure 7.4). Regression equations used to predict the frond frequency and size of invaded *D. antarctica* caudices returns values that are significantly higher than those actually measured (Table 7.8). Consequently invaded *D. antarctica* have smaller and fewer live fronds, and probably therefore a reduced photosynthetic capacity, than those not invaded with apogeotropic *Atherosperma moschatum* roots. Such morbidity to the degree evident (Table 7.8), is likely to reflect a considerable competitive disadvantage for the tree fern. Accordingly the allocation of resources for growth and reproduction is most likely reduced for *D. antarctica* caudices invaded by apogeotropic *Atherosperma moschatum* roots. Furthermore, since sori form on the lamina margins, a reduction in the size and number of fronds due to competitive root invasion of the caudex by another species can be expected to reduce the effective spore production in *D. antarctica*, compared to non-invaded individuals.

The demonstrated restorative capacity of the fern to recover from frond damage or destruction, due to drought, extremes of temperature including frosts, herbivory (although this is not often observed), or large falling debris, may also be affected by apogeotropic root invasion. Damage from large falling debris is not an uncommon event in the understorey of these moist forests and can be particularly debilitating to tree ferns due to the potential for removing the majority of live fronds. Although a tree fern, in all likelihood, will replace its fronds after these events, either immediately or when conditions are suitable, a series of damage events has the potential to progressively weaken the tree fern because its photosynthetic capacity will be reduced/removed over time and its energy reserve for replacement fronds becomes progressively more limited. The detriment of apogeotropic

Atherosperma moschatum root invasion to *D. antarctica* in such a scenario is that the tree fern is more likely to succumb to frond destruction, due to continuing productivity losses, than otherwise.

The inverse association between *D. antarctica* health and the intensity of apogeotropic invasion of *D. antarctica* indicates invaded *D. antarctica* comprise a greater proportion of dead *D. antarctica* caudices than that which would be expected through chance (Table 7.10). Although this suggests apogeotropic *Atherosperma moschatum* root invasion increases *D. antarctica* mortality, it is difficult to determine if invasion occurred before or after stem death. Mortality may not be related to apogeotropic root invasion, but instead the dead, decaying, and still erect *D. antarctica* caudices may persist and provide suitable conditions for apogeotropic *Atherosperma moschatum* root invasion. Therefore the perceived trend of increasing tree fern mortality with increasing invasion intensity by apogeotropic roots could instead be a trend of increasing invasion with time since death of the tree fern. It is also possible that as invasion intensity increases there is a greater likelihood for invaded *D. antarctica* to remain erect after death, through added structural support, that is death which may have resulted from a cause other than invasion by apogeotropic roots.

The detriment which invading apogeotropic *Atherosperma moschatum* roots can cause to *D. antarctica* is also shown by the effect on the tree fern's apical debris ring. Invading apogeotropic *Atherosperma moschatum* roots appear to result in the erosion of this structure and potentially the nutrient supply it represents. This is indicated by invaded *D. antarctica* possessing significantly shallower debris rings (median of 0.12 m) compared to non-invaded *D. antarctica* (median of 0.16 m). The reduction can be explained by observed host *D. antarctica* possessing comparatively smaller and fewer fronds since the rosette of fronds collects the debris (litter), and thereby maintains the debris ring's integrity. This leads both to reduced acquisition and retention of organic material and a smaller debris ring. The smaller debris rings of invaded tree ferns may seem to contradict the suggestion that

nutrients released from them are attracting apogeotropic *Atherosperma moschatum* roots. However, these measurements reflect the current debris ring length and not that which was present when root invasion began. In addition to its size the possible nutrient benefit, the debris ring's litter make-up, and its microbial and invertebrate activity, must be considered, as well as the status of other potential nutrient sources, such as the root mantle and soil.

Apogeotropic *Atherosperma moschatum* root invasion can be detrimental to *D. antarctica*. However without deep roots in the soil, *D. antarctica* specimens have the tendency to topple over when they reach excessive heights or when they develop a pronounced lean. Epiphytes and debris accumulations on the tree fern will contribute to this tendency as can wind, moisture and large falling debris. In such situations invading apogeotropic roots may confer a structural advantage to *D. antarctica* by adding anchorage and support to *D. antarctica* and hence may sometimes prevent them from falling over. This may allow *D. antarctica* to remain erect longer than in the absence of apogeotropic roots. It may also allow the fern to grow to a larger size, and produce a larger amount of spores (across its lifespan) compared to non-invaded *D. antarctica*. Furthermore the reduced frond frequency and frond size of invaded *D. antarctica* may make them less likely to be impacted by falling debris than for larger crowns of non-invaded caudices. *Dicksonia antarctica* is however quite hardy, for prostrate roots of a fallen caudex will grow into the soil and new fronds will orientate so the rosette faces upwards to restore an erect growth habit. Depending on microsite conditions, the ability of *D. antarctica* to recover from falls may thus reduce any benefit gained through added structural support by invading apogeotropic *Atherosperma moschatum* roots.

Conclusion

Atherosperma moschatum, *Acacia melanoxylon*, *Nothofagus cunninghamii*, and *Olearia argophylla* produce apogeotropic roots that invade the caudices of *D. antarctica*. Of these four tree species, *Atherosperma moschatum* is the most pervasive root invader of *D. antarctica* caudices. The majority of root-invaded *D. antarctica* caudices occurs in the

midrange size classes (> 1 m to ≤ 4.0 m caudex length), but the percentage of *D. antarctica* caudices invaded by apogeotropic *Atherosperma moschatum* roots increases with increasing size of the tree fern caudex. Non-invaded *D. antarctica* caudices in the larger size classes could have a greater mortality than invaded caudices in the same classes, which results in invaded caudices comprising a greater proportion of the total *D. antarctica* caudices in the larger size classes.

Root invasion by *Atherosperma moschatum* may be instigated when *Atherosperma moschatum* roots in the soil detect a locally higher concentration of nutrients in an adjacent medium, such as a *D. antarctica* caudex. The source for such nutrient concentration in the *D. antarctica* caudex may be its debris ring and/or its root mantle, either way there is a conduit of nutrient supply from the forest canopy, harvested by the rosette of fern fronds and transferred via the caudex to the soil. Further research is required to determine if and what nutrients in the *D. antarctica* caudex are providing a stimulus for apogeotropic *Atherosperma moschatum* root invasion. However, a link between apogeotropic *Atherosperma moschatum* root invasion and low soil nutrient availability is suggested by the significantly greater density of invaded *D. antarctica* caudices on soils of low fertility compared to those of high fertility. It is possible that *Atherosperma moschatum* roots in sites of low fertility invade a greater proportion of *D. antarctica* caudices compared to those on sites of high fertility, in order to maximise access to nutrients. Further research is required to confirm this explanation. The possibility that the higher general root biomass of the more fertile sites restricts the competitive ability of *Atherosperma moschatum* to reach and invade *D. antarctica* caudices is negated by the lack of a significant correlation between invaded *D. antarctica* caudex density and dominant tree density, and between invaded *D. antarctica* caudex density and the combined tree stem density of the two highest strata in the forest canopy.

Atherosperma moschatum stem density indicates a strong positive correlation with invaded *D. antarctica* caudex density. Non-invaded *D. antarctica* caudex density shows no

significant relationship with invaded *D. antarctica* caudex density. This discrepancy could be due to the likelihood of invasion varying with the nutritional status and condition among *D. antarctica* caudices or likewise among substantial *Atherosperma moschatum* invaders. Invaded *D. antarctica* are severely disadvantaged by apogeotropic root invasion, which is associated with a reduced frond size and frond frequency. Such a reduction is a significant disadvantage to the tree fern as it will limit its productivity and increase its susceptibility to periodic adverse conditions. Although greater mortality of *D. antarctica* caudices seems to increase with invasion intensity (Table 7.10) this could be misleading and instead a trend of increasing invasion intensity with time since death may exist.

Chapter 8: Synthesis and conclusion

Many species of vascular plant utilise the caudex of the tree fern *D. antarctica*. For instance *D. antarctica* is the principal host for at least 12 species of obligate epiphyte (Garrett 1996b). Furthermore plant species that are generally considered terrestrial (as opposed to epiphytic) have been reported as established on *D. antarctica* caudices, e.g. *Nothofagus cunninghamii*, *Atherosperma moschatum*, *Pittosporum bicolor* and *Coprosma quadrifida* (Ashton 2000, Garrett 1996b, Ough and Ross 1992), suggesting that it can exert a significant influence on forest structure and floristic composition. Apogeotropic roots of *Atherosperma moschatum* established on the forest floor have also been reported in the root mantle of erect *D. antarctica* caudices (Ashton 2000).

Unfortunately research into ecological relationships of *D. antarctica* is lacking, with the majority of published literature on the subject limited to brief field observations. The deficit of research into the ecology of *D. antarctica* limits present knowledge of the tree fern's functional role in contributing substantially to the diversity and dynamics of moist forest communities in south-eastern Australia. Comprehensive information is essential to facilitate the ecologically sustainable management of the legal *D. antarctica* harvest and horticultural trade in tree fern specimens as well as to define the extent and ecological risk of ecological damage that may result from poaching of the species (Figure 8.1).

This study fills a void in autoecological research of *D. antarctica* by investigating the epiphytic relationships between the tree ferns and those vascular plant species which utilise its caudex. During this study more than 1100 specimens of Soft Tree Fern (*D. antarctica*) were examined in 19 replicate field plot across moist forests of north-eastern Tasmania. Caudex condition and surface texture, the positions and floristics of vascular epiphytes and terrestrial (soil-borne) facultative colonisers, and frond and caudex dimensions of each tree fern specimen were recorded in plot sites of riverine and non-riverine locations of both low and high soil fertility. Species presence and abundance in the various forest strata were

recorded as were the position and crown spread of each *D. antarctica* specimen and canopy tree species in each sample site. The presence, height, overall intensity and species of apogeotropic roots in *D. antarctica* caudices were also recorded in what amounts to the most detailed and comprehensive investigation of the epiphytic relations of *D. antarctica* to date.



Figure 8.1 The absent upper caudex and growing apex of these *D. antarctica* caudices have been poached from State forest on Mt Arthur, Tasmania.

Twenty eight species of terrestrial flora and 11 species of obligate epiphyte were found to utilise large *D. antarctica* caudices as a regeneration substrate. Therefore *D. antarctica* caudices are important facilitators of biodiversity in the closed canopy wet forests of north-east Tasmania. The study also identified four tree species that produce apogeotropic roots that invade *D. antarctica* caudices. The prolific manner in which *D. antarctica* caudices are invaded by apogeotropic roots of *Atherosperma moschatum* was also recorded.

It was first considered necessary to examine frond plasticity in order to investigate the relationships between *D. antarctica* and its epiphytes. This is because epiphytes are likely to be influenced both by site climatic conditions and by their host's architecture (i.e. the

nature and conditions of the frond and caudex), which in turn also influence microsite conditions. Possible autocorrelation was thus considered when determining the effect of microclimate on the presence and diversity of obligate epiphytes on *D. antarctica*. How frond size, frond frequency and frond shape change as *D. antarctica* grows older and taller was examined. The inferred photosynthate store of *D. antarctica* was considered a critical determinant of emerging frond size and frequency in terms of frond production. Consequently the relationships shown by regression analysis between caudex length and the size, frequency and shape of fronds are most likely indirect. Caudex length and the size of the photosynthate store in the caudex are covariates and the direct relationship is likely to be between the photosynthate store and frond size and frond frequency.

Changes in the size, frequency and shape of fronds among respective binary low/high classes of canopy closure, maximum temperature and site fertility were identified by employing analysis of variance general linear model (ANOVA). Frond frequency, frond length, lamina length, upper lamina length, lower lamina length, upper lamina percentage of length, ratio of upper to lower lamina length, CAI and FAI all decreased from class 1 (low) to class 2 (high) canopy closure. Frond size and frond frequency were significantly greater on sites comprising fertility class 2 (high) compared to those sites comprising fertility class 1 (low). However no change occurred in the shape of fronds (represented by upper lamina percentage of length, lower lamina percentage of length, ratio of upper to lower lamina length, ratio of lamina width and length) between site fertility classes. Frond length, lamina width, lamina length, upper lamina length and FAI decreased from maximum temperature class 1 (low) to class 2 (high).

By employing Kruskal-Wallis tests *Dicksonia antarctica* caudices were identified as the dominant establishment substrate for *Atherosperma moschatum*, *Pittosporum bicolor* and *Tasmannia lanceolata*. Increased browsing by native fauna and subsequent death of *Atherosperma moschatum*, *Pittosporum bicolor* and possibly *Tasmannia lanceolata* on substrates lower than the erect tree fern caudex, such as soil, fallen *D. antarctica* caudices

and coarse woody debris were considered to be the cause. The continuation of *Pittosporum bicolor* and *Tasmannia lanceolata* in the sample sites under a closed canopy is dependent on the presence of suitable *D. antarctica* caudices upon which to establish. Of these species *Atherosperma moschatum* is less reliant than others on *D. antarctica* caudices for regeneration as it produces coppice frequently. However a lack of suitable establishment sites (such as large *D. antarctica* caudices) for seedling regeneration of *Atherosperma moschatum* could lead to the dominance of coppice and decline in the genetic diversity and health of *Atherosperma moschatum* populations.

Nothofagus cunninghamii can establish on all four substrates surveyed (i.e. erect *D. antarctica* caudices, fallen *D. antarctica* caudices, coarse woody debris or soil), provided there is sufficient insolation, but the results of the Kruskal-Wallis test showed that none dominates. The low browsing index of *Nothofagus cunninghamii* (Hickey 1982) was considered an important factor enhancing its survival on substrates closer to the ground as this would reduce its removal by native herbivores.

Olearia argophylla seedlings were prolific across all substrates in the conditions represented by the sample sites, but subsequent establishment success in general was poor and occurred only on soil and on erect *D. antarctica* caudices. The negative correlation of *Olearia argophylla* seedlings with combined subcanopy and canopy foliage cover (FPC) suggests young *Olearia argophylla* are essentially shade intolerant and hence a pioneer, gap opportunist and edge species. Therefore *Olearia argophylla* can only persist in rainforest due to long life and acclimation to shaded conditions, unless suitable exposed microsites are available (e.g. *D. antarctica* caudices), and seed release occurs proximate to those sites.

Coprosma quadrifida germination and establishment was predominantly on the forest soil, but still occurred on *D. antarctica* caudices. The frequencies and growth rates of all of the larger sized species of common facultative epiphyte are potentially suppressed by the nutritional constraints of the *D. antarctica* caudex, even though there can be the addition of

nutrients to the caudex through the concentration of water and litter in the apical debris ring.

Two main obligate epiphyte colonisation zones were identified on *D. antarctica* caudices, largely delineated by microclimate and substrate conditions. The first zone consists of the lower caudex and is dominated by hygrophytic vascular epiphytes, such as those of the filmy fern family Hymenophyllaceae, particularly *Crepidomanes venosum*. The lower caudex of *D. antarctica* is generally comprised of a rough textured, thick moisture retentive root mantle which the results of the Kruskal-Wallis test showed is associated with all the lower caudex zone epiphytes. The Kruskal-Wallis tests also showed that filmy fern species occurred at a greater frequency on the sheltered and shaded eastern and southern aspects of the caudex which feature the most mesic microsite conditions available. The importance of a mesic environment to the lower caudex zone epiphytes is highlighted by their significantly lower frequencies and lower diversity with increasing maximum temperature of the forest site, which was revealed by the results of ANOVA.

The second epiphyte colonisation zone is at the apex of the caudex, which is colonised by obligate epiphytes such as *Microsorium pustulatum* and *Rumohra adiantiformis* that can survive a drier more exposed microclimate compared to the lower caudex. The results of ANOVA showed no significant variation among high and low maximum temperature sites, indicating their resilience to the high temperatures experienced at the sample sites. The obligate epiphytes don't appear to tangle with the fronds of the *D. antarctica* crown and may help prevent the establishment of more damaging climbers. In between the lower caudex and caudex apex zones is typically a length of caudex largely devoid of obligate epiphytes. This section of caudex is probably shaded enough to prevent colonisation by the apical epiphytes but too dry to enable the survival of the lower caudex epiphytes.

Out of four tree species identified to produce apogeotropic roots that invade the caudex of *D. antarctica*, (i.e. *Atherosperma moschatum*, *Acacia melanoxylon*, *Nothofagus*

cunninghamii, and *Olearia argophylla*), *Atherosperma moschatum* is the most pervasive. Root invasion by *Atherosperma moschatum* may be instigated when *Atherosperma moschatum* roots in the soil detect a localised nutrient source of higher concentration in an adjacent *D. antarctica* caudex. The collection source for such a nutrient concentration in the *D. antarctica* caudex could be its debris ring and/or its root mantle, either way there is potentially a conduit of nutrient supply from the canopy via the rosette of fern fronds to the caudex and soil. Nutritional constraints potentially limit the growth rate of facultative epiphytes growing on the *D. antarctica* caudex, however continual flushing of nutrients down through the caudex by stemflow may create a gradient with sufficient concentration to attract apogeotropic roots.

A link between apogeotropic *Atherosperma moschatum* root invasion and low soil nutrient availability is shown by the results of ANOVA in the form of the significantly greater density of invaded *D. antarctica* caudices on sites of inferred low fertility compared to those of inferred high fertility. It is possible *Atherosperma moschatum* is maximising access to nutrients on sites of low fertility compared to those on sites of high fertility.

The results of ANOVA revealed a significantly greater predicted frond size and frequency compared to the actual measured frond size and frequency of *D. antarctica* invaded by apogeotropic roots. This is a significant disadvantage to the tree fern as it will limit its productivity and increase its susceptibility to periodic adverse conditions. Further research is required to determine if and what nutrients in the *D. antarctica* caudex are providing a stimulus for apogeotropic *Atherosperma moschatum* root invasion. The source of such nutrients also requires investigation, particularly the contribution a debris ring provides and if it influences *D. antarctica* productivity, colonisation by epiphytes and apogeotropic invasion.

Although *D. antarctica* is an important understorey dominant that influences forest diversity and structure across the field sites of this research, it is not a keystone species. As defined by Power *et al.* (1996):

—A keystone species is one whose effect is large, and disproportionately large relative to its abundance”.

Why isn't *D. antarctica* a keystone species? *Dicksonia antarctica* can be very abundant, with a density of up to 15 caudices per 100 m² being recorded in this study, dominating the understorey of a forest community when conditions are suitable. Therefore the effect of *D. antarctica* in mature wet forests (sampled in this thesis) is not disproportionately large relative to its abundance. The reasoning for this, in terms of forest diversity, is that although *D. antarctica* is a major host for vascular obligate epiphytes, especially lower strata epiphytes, most of these epiphyte species also occur on other substrates, such as mature and over mature canopy trees. Therefore the removal (natural or anthropogenic) of *D. antarctica* from a wet forest will not necessarily lead to the local extinction of those vascular obligate epiphyte species hosted by *D. antarctica*, only a reduction in their frequency. Certainly after *D. antarctica* removal the remaining epiphyte population, now largely on tree trunks with a lower moisture retention than *D. antarctica* caudices, will have a greater vulnerability to local extinction caused by desiccation. That vulnerability is evident in the declining frequencies and diversity of the lower strata epiphytes with increasing maximum temperature. Nevertheless, if *D. antarctica* caudices were removed from a wet forest, it is likely large assemblages of vascular obligate epiphytes would be restricted to very large mature and over mature trees, such as *Nothofagus cunninghamii*, in sheltered situations. Across larger tracks of wet forest, the removal of *D. antarctica* would likely result in the fragmentation of epiphyte populations.

In terms of the forest structure the removal of *D. antarctica* from where it was once abundant would increase insolation of the forest floor, resulting in the release of saplings and ground cover species that were once suppressed by the tree fern canopy. This effect although significant cannot be considered keystone, but is rather due to the tree fern's

dominance of the understorey. Even though the persistence of *Pittosporum bicolor* and *Tasmannia lanceolata* in mature wet forest is largely dependent on *D. antarctica*, the dominant canopy species *Nothofagus cunninghamii* and *Atherosperma moschatum* are not reliant on the tree fern for their persistence in mature forest. *Nothofagus cunninghamii* can regenerate on soil and coarse woody debris provided there is sufficient light and an absence of foraging lyre birds (McKenny and Kirkpatrick 1999). *Atherosperma moschatum* can regenerate via coppice in the absence of *D. antarctica* caudices.

Even though *D. antarctica* cannot be considered a keystone species it is still an important component of the forest. The contribution of *D. antarctica* to the maintenance of forest biodiversity and the population densities of important woody species suggests excessive harvesting of *D. antarctica* caudices, either legally or illegally, can be damaging to local forest diversity and structure. Even the excessive harvesting of smaller *D. antarctica* could delay recruitment into the larger size classes and limit the replacement of larger *D. antarctica*. As demonstrated, these specimens provide the dominant substrate for facultative and obligate epiphytes. The slow growth rate of *D. antarctica* further prolongs the replacement of especially large individuals (Forest Practices Authority 2007). Although legal harvesting is limited to salvage areas where forest is to be cleared (Forest Practices Authority 2007), illegal harvesting is under no such restriction and must be minimised lest the structure and floristic composition of accessible wet forests be altered for the long-term. However, the capacity for *D. antarctica* to survive relocation if handled appropriately suggests there is the potential to replant illegally harvested *D. antarctica* or to replace them with *D. antarctica* from cleared locations, provided it can be assured that transplanted caudices will not introduce disease to the new locale.

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Appendix 1

Appendix Table 1.1 Results of ANOVA ($\alpha \leq 0.05$) for *D. antarctica* morphological variables using multiple factors. Column “greater class” displays the class with the greater mean as well as the Tukey test p value. (***, $p \leq 0.001$; **, $p \leq 0.010$; *, $p \leq 0.05$; upper lamina length, lamina length from tip to maximum width; lower lamina length, lamina length from base to maximum width; upper lamina percentage of length, lamina length from tip to maximum width as a percentage of lamina length; lower lamina percentage of length, lamina length from base to maximum width as a percentage of lamina length; lamina width, lamina maximum width; FAI, frond area index; CAI, crown area index; ns, not significant; na, not applicable).

Response	Model Components		F	R-Sq(adj)	Class with greater mean
	Type	Variable			
Vertical canopy height	Covariate	Caudex erect length	57.16 ***	40.49%	na
	Covariate	Frond frequency	275.91 ***		na
	Covariate	Frond Length	157.55 ***		na
	Factor	All	ns		ns
Frond frequency	Covariate	Caudex erect length	431.71 ***	39.89%	na
	Factor	Canopy closure (1,2)	15.12 ***		1 ***
	Factor	Site fertility (1,2)	62.29 ***		2 ***
	Factor	Rainfall (1,2)	9.51 **		2 **
	Factor	Maximum temp (1,2)	15.49 ***		1 ***
	Factor	Minimum temp (1,2)	28.23 ***		2 ***
Frond length	Covariate	Caudex erect length	406.66 ***	34.81%	na
	Factor	Canopy closure (1,2)	16.10 ***		1 ***
	Factor	Site fertility (1,2)	21.62 ***		2 ***
	Factor	Maximum temp (1,2)	4.17 *		1 *
	Factor	Minimum temp (1,2)	10.89 ***		2 ***
Lamina width	Covariate	Caudex erect length	185.56 ***	24.16%	na
	Factor	Site fertility (1,2)	32.30 ***		2 ***
	Factor	Maximum temp (1,2)	33.95 ***		1 ***
	Factor	Minimum temp (1,2)	66.61 ***		2 ***

Table continued next page

Appendix Table 1.1 Continued

Response	Model Components		F	R-Sq(adj)	Class with greater mean
	Type	Variable			
Lamina length	Covariate	Caudex erect length	500.53 ***	39.95%	na
	Factor	Canopy closure (1,2)	26.25 ***		1 ***
	Factor	Site fertility (1,2)	26.19 ***		2 ***
	Factor	Maximum temp (1,2)	6.92 **		1 **
	Factor	Minimum temp (1,2)	14.21 ***		2 **
Upper lamina length	Covariate	Caudex erect length	239.94 ***	28.82%	na
	Factor	Canopy closure (1,2)	53.05 ***		1 ***
	Factor	Site fertility (1,2)	28.35 ***		2 ***
	Factor	Rainfall (1,2)	6.65 **		1 **
	Factor	Maximum temp (1,2)	27.78 ***		1 ***
	Factor	Minimum temp (1,2)	11.55 ***		2 ***
Lower lamina length	Covariate	Caudex erect length	412.52 ***	34.54%	na
	Factor	Canopy closure (1,2)	4.33 *		1 *
	Factor	Site fertility (1,2)	12.92 ***		2 ***
	Factor	Minimum temp (1,2)	19.45 ***		2 ***
Upper lamina percentage of length	Covariate	Caudex erect length	118.72 ***	14.16%	na
	Factor	Canopy closure (1,2)	5.65 **		1 **
Lower lamina percentage of length	Covariate	Caudex erect length	118.72 ***	14.16%	na
	Factor	Canopy closure (1,2)	5.65 **		2 **
Ratio of upper to lower lamina length	Covariate	Caudex erect length	119.28 ***	14.25%	na
	Factor	Canopy closure (1,2)	19.53 ***		1 ***
CAI	Covariate	Caudex erect length	526.03 ***	44.97 %	na
	Factor	Canopy closure (1,2)	21.68 ***		1 ***
	Factor	Site fertility (1,2)	70.96 ***		2 ***
	Factor	Rainfall (1,2)	7.50 **		2 ***
	Factor	Maximum temp (1,2)	23.53 ***		1 ***
	Factor	Minimum temp (1,2)	49.99 ***		2 ***

Table continued next page

Appendix Table 1.1 Continued

Response	Model Components		F	R-Sq(adj)	Class with greater mean
	Type	Variable			
ratio of lamina width and length	Covariate	Caudex erect length	349.16 ***	33.14%	na
	Factor	Canopy closure (1,2)	43.03 ***		2 ***
	Factor	Rainfall (1,2)	7.52 **		2 **
FAI	Covariate	Caudex erect length	416.63 ***	36.36%	na
	Factor	Canopy closure (1,2)	15.58 ***		1 ***
	Factor	Site fertility (1,2)	36.40 ***		2 ***
	Factor	Maximum temp (1,2)	17.49 ***		1 ***
	Factor	Minimum temp (1,2)	37.94 ***		2 ***

Appendix 2

Appendix Table 2.1 Results of ANOVA ($\alpha \leq 0.05$). Response: Site epiphyte species frequency, Factors: Canopy closure, rainfall, maximum temperature, canopy height and site fertility. Where ANOVA identified the classes of a factor or covariate as possessing no significant variation that variable was removed and the model recalculated. Column “greater class” displays which of the two classes is the greater and the Tukey test p value. (***, $p \leq 0.001$; **, $p \leq 0.01$; ns, not significant; na, not applicable).

Frequency	Model Components		F	R-Sq(adj)	Class with greater mean
	Type	Variable			
<i>Crepidomanes venosum</i>	Covariate	≥ 1 m caudex density	ns	30.36 %	na
	Factor	Canopy closure (1,2)	ns		ns
	Factor	Rainfall (1,2)	ns		ns
	Factor	Maximum temp (1,2)	8.85 **		1 **
	Factor	Canopy height (1,2)	ns		ns
	Factor	Site Fertility (1,2)	ns		ns
<i>Grammitis billardierei</i>	Covariate	≥ 1 m caudex density	ns	53.54 %	ns
	Factor	Canopy closure (1,2)	ns		ns
	Factor	Rainfall (1,2)	ns		ns
	Factor	Maximum temp (1,2)	21.74 ***		1 ***
	Factor	Canopy height (1,2)	ns		ns
	Factor	Site Fertility (1,2)	ns		ns
<i>Hymenophyllum flabellatum</i>	Covariate	≥ 1 m caudex density	ns	66.17%	ns
	Factor	Canopy closure (1,2)	ns		ns
	Factor	Rainfall (1,2)	ns		ns
	Factor	Maximum temp (1,2)	36.21 ***		1 ***
	Factor	Canopy height (1,2)	ns		ns
	Factor	Site Fertility (1,2)	ns		ns
<i>Microsorium pustulatum</i>	Covariate	≥ 1 m caudex density	37.01 ***	74.69%	na
	Factor	Canopy closure (1,2)	ns		ns
	Factor	Rainfall (1,2)	ns		ns
	Factor	Maximum temp (1,2)	ns		ns
	Factor	Canopy height (1,2)	6.58 ***		1 **
	Factor	Site Fertility (1,2)	ns		ns

Table continued next page

Appendix Table 2.1 Continued

Frequency	Model Components		F	R-Sq(adj)	Class with greater mean
	Type	Variable			
<i>Rumohra adiantiformis</i>	Covariate	caudex density	16.18 ***	na	na
	Factor	Canopy closure (1,2)	ns		ns
	Factor	Rainfall (1,2)	ns		ns
	Factor	Maximum temp (1,2)	ns		ns
	Factor	Canopy height (1,2)	ns		ns
	Factor	Site Fertility (1,2)	ns		ns
Species richness	Covariate	≥ 3 m caudex density	ns	76.93%	na
	Factor	Canopy closure (1,2)	ns		ns
	Factor	Rainfall (1,2)	ns		ns
	Factor	Maximum temp (1,2)	61.01 ***		1 ***
	Factor	Canopy height (1,2)	ns		ns
	Factor	Site Fertility (1,2)	ns		ns

Appendix 3

Appendix Table 3.1 Kruskal-Wallis test results (adjusted for ties) α 0.05. Comparison of the frequency of common facultative epiphyte species upon each substrate and across each of the 3 facultative epiphyte size classes (< 0.20 m, ≥ 0.20 to < 3 m, and ≥ 3 m tall). The substrate present in the result cell possesses the greater rank of the two classes compared if a significant variation was identified. NA is in the cell when the frequency on both substrates is 0 (Table E). (DaC, Erect *D. antarctica* caudex; FC, Fallen *D. antarctica* caudex; CWD, Coarse woody debris; Soil, Soil and litter; Cop, Coppice; Elev, Elevated substrates; NA, not applicable).

(a) <i>A. moschatum</i> < 0.20 m tall					
Substrate	DaC	FC	CWD	DaC&FC	Elev
FC	H = 0.60 p = 0.437				
CWD	H = 0.67 p = 0.414	H = 0.01 p = 0.917		H = 0.32 p = 0.573	
Soil	H = 1.55 p = 0.213	H = 2.73 p = 0.099	H = 2.58 p = 0.108	H = 4.7 p = 0.03 DaC&FC	H = 5.38 p = 0.020 Elev

(b) <i>A. moschatum</i> height class ≥ 0.20 m to < 3.0 m tall						
	DaC	FC	CWD	Soil	DaC&FC	Elev
FC	H = 8.62 p = 0.003 DaC					
CWD	H = 11.72 p \leq 0.001 DaC	H = 1.00 p = 0.317			H = 11.72 p \leq 0.001 DaC&FC	
Soil	H = 8.23 p = 0.004 DaC	H = 0.00 p = 0.964	H = 1.00 p = 0.32		H = 8.23 p = 0.004 DaC&FC	H = 8.23 p = 0.004 Elev
Cop	H = 0.18 p = 0.675	H = 6.72 p = 0.010 Cop	H = 10.07 p = 0.02 Cop	H = 6.59 p = 0.010 Cop	H = 0.18 p = 0.675	H = 0.18 p = 0.675

(c) <i>A. moschatum</i> height class ≥ 3.0 m tall						
	DaC	FC	CWD	Soil	DaC&FC	All Subs
FC	H = 0.60 p = 0.437					
CWD	H = 4.34 p = 0.037 DaC	H = 3.72 p = 0.054 FC			H = 6.96 p = 0.008 DaC&FC	
Soil	H = 4.71 p = 0.030 Soil	H = 8.27 p = 0.004 Soil	H = 14.97 p \leq 0.001 Soil		H = 1.72 p = 0.190	
Cop	H = 1.12 p = 0.289	H = 1.45 p = 0.228	H = 7.34 p = 0.07 Cop	H = 0.75 p = 0.386	H = 0.18 p = 0.672	H = 2.63 p = 0.105

Table continued next page

Appendix Table 3.1 Continued

(d) <i>Coprosma quadrifida</i> height class < 0.20 m tall						(e) <i>Coprosma quadrifida</i> height class \geq 0.20 m tall					
	DaC	FC	CWD	DaC&FC	Elev		DaC	FC	CWD	DaC&FC	Elev
FC	H = 2.36 p = 0.125					FC	NA				
CWD	H = 0.31 p = 0.579	H = 2.25 p = 0.134		H = 0.12 p = 0.734		CWD	NA	NA		NA	
Soil	H = 6.06 p = 0.014 Soil	H = 8.30 p = 0.004 Soil	H = 8.30 p = 0.004 Soil	H = 3.54 p = 0.06 Soil	H = 0.96 p = 0.328	Soil	H = 0.47 p = 0.491	NA	NA	NA	NA

Table continued next page

Appendix Table 3.1 Continued

(f) <i>N. cunninghamii</i> height class < 0.20 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	H = 1.13 p = 0.288				
CWD	H = 4.37 p = 0.037 CWD	H = 5.65 p = 0.017 CWD		H = 1.96 p = 0.161	
Soil	H = 1.40 p = 0.237	H = 2.97 p = 0.085	H = 0.17 p = 0.681	H = 0.27 p = 0.601	H = 1.04 p = 0.307

(g) <i>N. cunninghamii</i> height class ≥ 0.20 m to < 3.0 m tall						
	DaC	FC	CWD	Soil	DaC&FC	Elev
FC	H = 3.19 p = 0.074					
CWD	H = 0.97 p = 0.325	H = 1.00 p = 0.317			H = 3.16 p = 0.076	
Soil	H = 0.11 p = 0.737	H = 2.06 p = 0.151	H = 0.40 p = 0.529		H = 0.11 p = 0.737	H = 0.53 p = 0.468
Cop	H = 0.12 p = 0.733	H = 4.39 p = 0.036 Cop	H = 1.88 p = 0.170	H = 0.61 p = 0.437	H = 0.12 p = 0.733	H = 0.01 p = 0.908

(h) <i>N. cunninghamii</i> height class ≥ 3.0 m tall						
	DaC	FC	CWD	Soil	DaC&FC	All Subs
FC	H = 1.04 p = 0.308					
CWD	H = 1.43 p = 0.232	H = 0.11 p = 0.737			H = 3.16 p = 0.76	
Soil	H = 11.28 p ≤ 0.001 Soil	H = 17.03 p ≤ 0.001 Soil	H = 16.72 p ≤ 0.001 Soil		H = 9.93 p = 0.002 Soil	
Cop	H = 2.55 p = 0.111	H = 6.71 p = 0.010 Cop	H = 7.22 p = 0.007 Cop	H = 6.61 p = 0.010 Soil	H = 1.28 p = 0.259	H = 10.59 p ≤ 0.001 All Subs

Table continued next page

Appendix Table 3.1 Continued

(i) <i>O. argophylla</i> height class < 0.20 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	H = 4.52 p = 0.033 DaC				
CWD	H = 7.59 p = 0.006 DaC	H = 0.52 p = 0.472		H = 8.96 p = 0.003 DaC&FC	
Soil	H = 0.11 p = 0.741	H = 3.10 p = 0.078	H = 4.89 p = 0.027 Soil	H = 0.72 p = 0.395	H = 0.79 p = 0.374

(j) <i>O. argophylla</i> height class ≥ 0.20 m to < 3.0 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	NA	NA	NA	NA	NA
CWD	NA	NA	NA	NA	NA
Soil	H = 0.25 p = 0.620	NA	NA	NA	NA

(k) <i>O. argophylla</i> height class ≥ 3.0 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	NA	NA	NA	NA	NA
CWD	NA	NA	NA	NA	NA
Soil	H = 7.54 p = 0.006 Soil	NA	NA	NA	NA

Table continued next page

Appendix Table 3.1 Continued

(l) <i>P. bicolor</i> height class < 0.20 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	H = 9.54 p = 0.002 DaC				
CWD	H = 4.23 p = 0.04 DaC	H = 0.61 p = 0.436		H = 4.75 p = 0.029 DaC&FC	
Soil	H = 0.34 p = 0.561	H = 5.64 p = 0.018 Soil	H = 2.74 p = 0.098	H = 0.08 p = 0.777	H = 0.21 p = 0.645

(m) <i>P. bicolor</i> height class ≥ 0.20 m to < 3.0 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	H = 27.90 p ≤ 0.001 DaC				
CWD	H = 27.90 p ≤ 0.001 DaC	H = 0.00 p = 1.00		H = 28.06 p ≤ 0.001 DaC&FC	
Soil	H = 14.82 p ≤ 0.001 DaC	H = 4.41 p = 0.036 Soil	H = 4.41 p = 0.036 Soil	H = 15.26 p ≤ 0.001 DaC&FC	H = 15.26 p ≤ 0.001 Elev

(n) <i>P. bicolor</i> height class ≥ 3.0 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	H = 10.07 p = 0.002 DaC				
CWD	H = 14.57 p ≤ 0.001 DaC	H = 2.06 p = 0.152		H = 18.34 p ≤ 0.001 DaC&FC	
Soil	H = 0.01 p = 0.938	H = 8.30 p = 0.04 Soil	H = 12.87 p ≤ 0.001 Soil	H = 0.26 p = 0.613	H = 0.26 p = 0.613

Table continued next page

Appendix Table 3.1 Continued

(o) <i>T. lanceolata</i> height class < 0.20 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	H = 2.58 p = 0.108				
CWD	H = 2.58 p = 0.108	H = 0.01 p = 0.923		H = 4.05 p = 0.044 DaC&FC	
Soil	H = 0.58 p = 0.446	H = 0.61 p = 0.436	H = 0.70 p = 0.402	H = 1.12 p = 0.291	H = 2.33 p = 0.127

(p) <i>T. lanceolata</i> height class \geq 0.20 m to < 3.0 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	H = 9.16 p = 0.002 DaC				
CWD	H = 7.79 p = 0.005 DaC	H = 0.01 p = 0.940		H = 7.79 p = 0.005 DaC&FC	
Soil	H = 10.53 p \leq 0.001 DaC	H = 0.36 p = 0.549	H = 0.41 p = 0.521	H = 10.53 p \leq 0.001 DaC&FC	H = 12.41 p \leq 0.001 Elev

(q) <i>T. lanceolata</i> height class \geq 3.0 m tall					
	DaC	FC	CWD	DaC&FC	Elev
FC	H = 0.09 p = 0.762				
CWD	H = 1.28 p = 0.257	H = 2.20 p = 0.138		H = 6.34 p = 0.012 DaC&FC	
Soil	H = 0.40 p = 0.526	H = 0.10 p = 0.751	H = 2.40 p = 0.122	H = 0.39 p = 0.530	H = 0.43 p = 0.514

Appendix 4

Appendix Table 4.1 Spearman's Rank Correlation of common facultative epiphyte species < 0.20 m tall, ≥ 0.20 m tall and All (combination of < 0.20 m tall and ≥ 0.20 m tall) on *D. antarctica* caudices versus *D. antarctica* morphological variables. The correlations have been repeated for each. (CAI, crown area index, *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$; ns, not significant).

Frequency in each species size class	<i>D. antarctica</i> Variable	Correlation Result
<i>Atherosperma moschatum</i> < 0.20 m tall	Caudex rough textured length	0.145***
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	Caudex rough textured length	0.249***
<i>Atherosperma moschatum</i> All	Caudex rough textured length	0.284***
<i>Atherosperma moschatum</i> < 0.20 m tall	Max diameter	0.148***
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	Max diameter	0.238***
<i>Atherosperma moschatum</i> All	Max diameter	0.282***
<i>Atherosperma moschatum</i> < 0.20 m tall	Erect caudex length	0.151***
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	Erect caudex length	0.286***
<i>Atherosperma moschatum</i> All	Erect caudex length	0.315***
<i>Atherosperma moschatum</i> < 0.20 m tall	Frond frequency	0.028 ns
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	Frond frequency	0.063 ns
<i>Atherosperma moschatum</i> All	Frond frequency	0.081*
<i>Atherosperma moschatum</i> < 0.20 m tall	Residual frond frequency	- 0.071*
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	Residual frond frequency	-0.005 ns
<i>Atherosperma moschatum</i> All	Residual frond frequency	-0.022 ns
<i>Atherosperma moschatum</i> < 0.20 m tall	CAI	0.039 ns
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	CAI	0.048 ns
<i>Atherosperma moschatum</i> All	CAI	0.074*
<i>Nothofagus cunninghamii</i> < 0.20 m tall	Max diameter	0.053 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	Max diameter	0.140***
<i>Nothofagus cunninghamii</i> All	Max diameter	0.127***
<i>Nothofagus cunninghamii</i> < 0.20 m tall	Erect caudex length	0.065*
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	Erect caudex length	0.159***
<i>Nothofagus cunninghamii</i> All	Erect caudex length	0.147***
<i>Nothofagus cunninghamii</i> < 0.20 m tall	Caudex rough textured length	0.034 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	Caudex rough textured length	0.122***
<i>Nothofagus cunninghamii</i> All	Caudex rough textured length	0.108***
<i>Nothofagus cunninghamii</i> < 0.20 m tall	Frond frequency	-0.004 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	Frond frequency	-0.018 ns
<i>Nothofagus cunninghamii</i> All	Frond frequency	-0.004 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall	Residual frond frequency	0.044 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	Residual frond frequency	0.001 ns
<i>Nothofagus cunninghamii</i> All	Residual frond frequency	0.050 ns

Table continued next page

Appendix Table 4.1 Continued

Frequency in each species size class	<i>D. antarctica</i> Variable	Correlation Result
<i>Nothofagus cunninghamii</i> < 0.20 m tall	CAI	-0.028 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	CAI	-0.014 ns
<i>Nothofagus cunninghamii</i> All	CAI	-0.031 ns
<i>Coprosma quadrifida</i> All	Max diameter	0.007 ns
<i>Coprosma quadrifida</i> < 0.20 m tall	Max diameter	0.002 ns
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	Max diameter	0.014 ns
<i>Coprosma quadrifida</i> All	Erect caudex length	0.085*
<i>Coprosma quadrifida</i> < 0.20 m tall	Erect caudex length	0.064 ns
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	Erect caudex length	0.077*
<i>Coprosma quadrifida</i> All	Caudex rough textured length	0.089*
<i>Coprosma quadrifida</i> < 0.20 m tall	Caudex rough textured length	0.069 ns
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	Caudex rough textured length	0.089*
<i>Coprosma quadrifida</i> All	Fronde frequency	0.027 ns
<i>Coprosma quadrifida</i> < 0.20 m tall	Fronde frequency	0.016 ns
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	Fronde frequency	0.027 ns
<i>Coprosma quadrifida</i> All	Residual fronde frequency	0.098*
<i>Coprosma quadrifida</i> < 0.20 m tall	Residual fronde frequency	0.074 ns
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	Residual fronde frequency	0.090*
<i>Coprosma quadrifida</i> All	CAI	0.042 ns
<i>Coprosma quadrifida</i> < 0.20 m tall	CAI	0.033 ns
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	CAI	0.029 ns
<i>Pittosporum bicolor</i> < 0.20 m tall	Max diameter	0.070***
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	Max diameter	0.164***
<i>Pittosporum bicolor</i> All	Max diameter	0.174***
<i>Pittosporum bicolor</i> < 0.20 m tall	Erect caudex length	0.133***
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	Erect caudex length	0.215***
<i>Pittosporum bicolor</i> All	Erect caudex length	0.243***
<i>Pittosporum bicolor</i> < 0.20 m tall	Caudex rough textured length	0.117***
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	Caudex rough textured length	0.207***
<i>Pittosporum bicolor</i> All	Caudex rough textured length	0.227***
<i>Pittosporum bicolor</i> < 0.20 m tall	Fronde frequency	0.055 ns
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	Fronde frequency	0.096***
<i>Pittosporum bicolor</i> All	Fronde frequency	0.122***
<i>Pittosporum bicolor</i> < 0.20 m tall	Residual fronde frequency	0.050 ns
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	Residual fronde frequency	0.030 ns
<i>Pittosporum bicolor</i> All	Residual fronde frequency	0.066*
<i>Pittosporum bicolor</i> < 0.20 m tall	CAI	-0.003 ns
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	CAI	0.082**
<i>Pittosporum bicolor</i> All	CAI	0.078**

Table continued next page

Appendix Table 4.1 Continued

Frequency in each species size class	<i>D. antarctica</i> Variable	Correlation Result
<i>Tasmannia lanceolata</i> < 0.20 m tall	Max diameter	0.072 *
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	Max diameter	0.131 ***
<i>Tasmannia lanceolata</i> All	Max diameter	0.139 ***
<i>Tasmannia lanceolata</i> < 0.20 m tall	Erect caudex length	0.130 ***
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	Erect caudex length	0.181 ***
<i>Tasmannia lanceolata</i> All	Erect caudex length	0.218 ***
<i>Tasmannia lanceolata</i> < 0.20 m tall	Caudex rough textured length	0.121 ***
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	Caudex rough textured length	0.165 ***
<i>Tasmannia lanceolata</i> All	Caudex rough textured length	0.195 ***
<i>Tasmannia lanceolata</i> < 0.20 m tall	Frond frequency	0.135 ***
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	Frond frequency	0.120 ***
<i>Tasmannia lanceolata</i> All	Frond frequency	0.164 ***
<i>Tasmannia lanceolata</i> < 0.20 m tall	Residual frond frequency	0.047 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	Residual frond frequency	0.005 ns
<i>Tasmannia lanceolata</i> All	Residual frond frequency	0.029 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall	CAI	0.069*
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	CAI	0.056 ns
<i>Tasmannia lanceolata</i> All	CAI	0.074 *
<i>Olearia argophylla</i> < 0.20 m tall	Max diameter	0.135 ***
<i>Olearia argophylla</i> ≥ 0.20 m tall	Max diameter	0.083*
<i>Olearia argophylla</i> All	Max diameter	0.142***
<i>Olearia argophylla</i> < 0.20 m tall	Erect caudex length	0.165***
<i>Olearia argophylla</i> ≥ 0.20 m tall	Erect caudex length	0.118***
<i>Olearia argophylla</i> All	Erect caudex length	0.180***
<i>Olearia argophylla</i> < 0.20 m tall	Caudex rough textured length	0.189***
<i>Olearia argophylla</i> ≥ 0.20 m tall	Caudex rough textured length	0.106**
<i>Olearia argophylla</i> All	Caudex rough textured length	0.200 ***
<i>Olearia argophylla</i> < 0.20 m tall	Frond frequency	0.148**
<i>Olearia argophylla</i> ≥ 0.20 m tall	Frond frequency	0.058 ns
<i>Olearia argophylla</i> All	Frond frequency	0.149***
<i>Olearia argophylla</i> < 0.20 m tall	Residual frond frequency	0.132***
<i>Olearia argophylla</i> ≥ 0.20 m tall	Residual frond frequency	0.034 ns
<i>Olearia argophylla</i> All	Residual frond frequency	0.133***
<i>Olearia argophylla</i> < 0.20 m tall	CAI	0.074*
<i>Olearia argophylla</i> ≥ 0.20 m tall	CAI	0.037 ns
<i>Olearia argophylla</i> All	CAI	0.086**

Appendix 5

Appendix Table 5.1 Kruskal-Wallis test results (adjusted for ties). Comparison of the frequency of common facultative epiphyte species (< 0.20 m and ≥ 0.20 m) upon *D. antarctica* caudices among the three *D. antarctica* erect caudex length size classes i.e. Class 1, Caudex length < 2 m; Class 2, Caudex length ≥ 2 m to < 3 m; Class 3, Caudex length ≥ 3 m; (ns, not significant).

Frequency on <i>D. antarctica</i> caudices	Caudex size class	Average rank	Result
<i>Atherosperma moschatum</i> < 0.20 m tall	1	ns	H = 2.16 df = 1 p = 0.142
	2	ns	
<i>Atherosperma moschatum</i> < 0.20 m tall	1	370.1	H = 22.44 df = 1 p ≤ 0.001
	3	394.4	
<i>Atherosperma moschatum</i> < 0.20 m tall	2	192.5	H = 5.15 df = 1 p = 0.023
	3	202.4	
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	1	ns	H = 1.42 df = 1 p = 0.234
	2	ns	
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	1	358.2	H = 93.70 df = 1 p ≤ 0.001
	3	427.4	
<i>Atherosperma moschatum</i> ≥ 0.20 m tall	2	178.5	H = 41.00 df = 1 p ≤ 0.001
	3	216.1	
<i>Nothofagus cunninghamii</i> < 0.20 m tall	1	ns	H = 1.69 df = 1 p = 0.193
	2	ns	
<i>Nothofagus cunninghamii</i> < 0.20 m tall	1	388.3	H = 4.59 df = 1 p = 0.032
	3	402.9	
<i>Nothofagus cunninghamii</i> < 0.20 m tall	2	198.4	H = 7.28 df = 1 p = 0.007
	3	209.9	
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	1	ns	H = 0.49 df = 1 p = 0.486
	2	ns	
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	1	386.0	H = 26.83 df = 1 p ≤ 0.001
	3	409.6	
<i>Nothofagus cunninghamii</i> ≥ 0.20 m tall	2	198.4	H = 8.93 df = 1 p = 0.003
	3	209.8	
<i>Coprosma quadrifida</i> < 0.20 m tall	1	282.4	H = 5.40 df = 1 p = 0.020
	2	297.8	
<i>Coprosma quadrifida</i> < 0.20 m tall	1	ns	H = 0.00 df = 1 p = 0.946
	3	ns	
<i>Coprosma quadrifida</i> < 0.20 m tall	2	ns	H = 2.54 df = 1 p = 0.111
	3	ns	
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	1	281.6	H = 17.16 df = 1 p ≤ 0.001
	2	300.9	
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	1	278.1	H = 0.922 df = 1 p = 0.01
	3	277.7	

Table continued next page

Appendix Table 5.1 Continued

Frequency on <i>D. antarctica</i> caudices	Caudex Size class	Average rank	Result
<i>Coprosma quadrifida</i> ≥ 0.20 m tall	2	112.4	H = 5.63 df = 1
	3	105.1	p = 0.018
<i>Pittosporum bicolor</i> < 0.20 m tall	1	331.2	H = 4.73 df = 1
	2	340.3	p = 0.03
<i>Pittosporum bicolor</i> < 0.20 m tall	1	396.8	H = 14.77 df = 1
	3	420.1	p \leq 0.001
<i>Pittosporum bicolor</i> < 0.20 m tall	2	ns	H = 2.98 df = 1
	3	ns	p = 0.084
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	1	328.8	H = 10.04 df = 1
	2	343.1	p = 0.002
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	1	382.1	H = 39.84 df = 1
	3	431.4	p \leq 0.001
<i>Pittosporum bicolor</i> ≥ 0.20 m tall	2	371.9	H = 12.60 df = 1
	3	402.3	p \leq 0.001
<i>Tasmannia lanceolata</i> < 0.20 m tall	1	ns	H = 0.00 df = 1
	2	ns	p = 1.00
<i>Tasmannia lanceolata</i> < 0.20 m tall	1	ns	H = 17.79 df = 1
	3	327.6	p \leq 0.001
<i>Tasmannia lanceolata</i> < 0.20 m tall	2	299.5	H = 16.85 df = 1
	3	320.1	p \leq 0.001
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	1	ns	H = 0.00 df = 1
	2	ns	p = 1.00
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	1	304.0	H = 21.53 df = 1
	3	329.3	p \leq 0.001
<i>Tasmannia lanceolata</i> ≥ 0.20 m tall	2	2971.0	H = 20.38 df = 1
	3	321.7	p \leq 0.001
<i>Olearia argophylla</i> < 0.20 m tall	1	275.6	H = 10.20 df = 1
	2	291.6	p = 0.001
<i>Olearia argophylla</i> < 0.20 m tall	1	326.9	H = 24.34 df = 1
	3	361.8	p \leq 0.001
<i>Olearia argophylla</i> < 0.20 m tall	2	ns	H = 3.16 df = 1
	3	ns	p = 0.075
<i>Olearia argophylla</i> ≥ 0.20 m tall	1	ns	H = 3.48 df = 1
	2	ns	p = 0.062
<i>Olearia argophylla</i> ≥ 0.20 m tall	1	342.0	H = 7.09 df = 1
	3	350.0	p = 0.008
<i>Olearia argophylla</i> ≥ 0.20 m tall	2	ns	H = 3.32 df = 1
	3	ns	p = 0.068

Appendix 6

Appendix Table 6.1 Spearman's Rank Correlation of common facultative epiphyte species frequency < 0.20 m tall and ≥ 0.20 m tall on each substrate with the FPC median value of separate and combined stratum/s. (GC, ground cover stratum; LUS, lower understorey stratum; HUS, higher understorey stratum; C, canopy stratum; All, all strata combined; Soil, soil/litter; CWD, coarse woody debris; FC, fallen *D. antarctica* caudices; DaC, erect *D. antarctica* caudices; All Sub, all substrates; *, $p \leq 0.05$; ns, not significant; na, not applicable).

Frequency	Stratum/s	Correlation Result
<i>Atherosperma moschatum</i> < 0.20 m tall (All Sub)	GC	-0.198 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (All Sub)	GC & LUS	-0.022 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (All Sub)	LUS to C	0.047 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (All Sub)	HUS to C	0.020 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (All Sub)	All	0.011 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (Soil)	GC	-0.134 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (Soil)	All	-0.138 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (CWD)	LUS to C	0.094 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (CWD)	All	-0.107 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (FC)	LUS to C	0.060 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (FC)	All	-0.107 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (DaC)	LUS to C	-0.323 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (DaC)	HUS to C	-0.332 ns
<i>Atherosperma moschatum</i> < 0.20 m tall (DaC)	All	-0.329 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (All Sub)	GC	-0.503 *
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (All Sub)	GC & LUS	-0.336 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (All Sub)	LUS to C	0.160 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (All Sub)	HUS to C	0.117 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (All Sub)	All	-0.129 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (Soil)	GC	-0.228 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (Soil)	All	0.028 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (CWD)	LUS to C	NA
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (CWD)	All	NA
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (FC)	LUS to C	0.141 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (FC)	All	-0.028 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (DaC)	LUS to C	0.154 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (DaC)	HUS to C	0.148 ns
<i>Atherosperma moschatum</i> ≥ 0.20 to < 3 m tall (DaC)	All	-0.125 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (All Sub)	GC	-0.050 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (All Sub)	GC & LUS	0.020 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (All Sub)	LUS to C	-0.157 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (All Sub)	HUS to C	-0.430 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (All Sub)	All	-0.309 ns

Table continued next page

Appendix Table 6.1 Continued

Frequency	Stratum/s	Correlation Result
<i>Nothofagus cunninghamii</i> < 0.20 m tall (Soil)	GC	-0.111 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (Soil)	All	-0.213 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (CWD)	LUS to C	-0.333 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (CWD)	All	-0.332 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (FC)	LUS to C	-0.062 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (FC)	All	-0.120 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (DaC)	LUS to C	-0.196 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (DaC)	HUS to C	-0.307 ns
<i>Nothofagus cunninghamii</i> < 0.20 m tall (DaC)	All	-0.105 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (All Sub)	GC	0.022 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (All Sub)	GC & LUS	0.012 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (All Sub)	LUS to C	-0.236 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (All Sub)	HUS to C	-0.444 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (All Sub)	All	-0.330 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (Soil)	GC	0.212 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (Soil)	LUS to C	0.033 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (Soil)	All	0.022 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (CWD)	LUS to C	-0.205 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (CWD)	All	-0.077 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (FC)	LUS to C	NA
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (FC)	All	NA
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (DaC)	LUS to C	-0.205 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (DaC)	HUS to C	0.103 ns
<i>Nothofagus cunninghamii</i> ≥ 0.20 to < 3 m tall (DaC)	All	-0.077 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (All Sub)	GC	0.538 *
<i>Coprosma quadrifida</i> < 0.20 m tall (All Sub)	GC & LUS	0.616 *
<i>Coprosma quadrifida</i> < 0.20 m tall (All Sub)	LUS to C	0.214 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (All Sub)	HUS to C	-0.160 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (All Sub)	All	0.412 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (Soil)	GC	0.518 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (Soil)	All	0.426 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (CWD)	LUS to C	0.146 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (CWD)	All	0.215 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (FC)	LUS to C	0.202 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (FC)	All	0.182 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (DaC)	LUS to C	0.101 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (DaC)	HUS to C	-0.208 ns
<i>Coprosma quadrifida</i> < 0.20 m tall (DaC)	All	0.353 ns

Table continued next page

Appendix Table 6.1 Continued

Frequency	Stratum/s	Correlation Result
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (All Sub)	GC	0.284 ns
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (All Sub)	GC & LUS	0.604 *
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (All Sub)	LUS to C	0.258 ns
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (All Sub)	HUS to C	-0.312 ns
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (All Sub)	All	0.252 ns
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (Soil)	GC	0.441 ns
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (Soil)	All	0.445 ns
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (CWD)	LUS to C	NA
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (CWD)	All	NA
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (FC)	LUS to C	NA
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (FC)	All	NA
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (DaC)	LUS to C	0.181 ns
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (DaC)	HUS to C	-0.124 ns
<i>Coprosma quadrifida</i> ≥ 0.20 to < 3 m tall (DaC)	All	0.021 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (All Sub)	GC	0.006 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (All Sub)	GC & LUS	-0.032 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (All Sub)	LUS to C	-0.050 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (All Sub)	HUS to C	0.081 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (All Sub)	All	0.076 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (Soil)	GC	0.225 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (Soil)	All	0.346 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (CWD)	LUS to C	-0.072 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (CWD)	All	0.080 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (FC)	LUS to C	-0.066 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (FC)	All	-0.145 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (DaC)	LUS to C	0.280 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (DaC)	HUS to C	0.228 ns
<i>Pittosporum bicolor</i> < 0.20 m tall (DaC)	All	0.280 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (All Sub)	GC	-0.142 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (All Sub)	GC & LUS	0.254 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (All Sub)	LUS to C	0.276 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (All Sub)	HUS to C	-0.165 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (All Sub)	All	0.073 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (Soil)	GC	0.284 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (Soil)	All	-0.050 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (CWD)	LUS to C	-0.065 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (CWD)	All	0.022 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (FC)	LUS to C	0.022 ns

Table continued next page

Appendix Table 6.1 Continued

Frequency	Stratum/s	Correlation Result
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (FC)	All	0.173 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (DaC)	LUS to C	0.299 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (DaC)	HUS to C	0.032 ns
<i>Pittosporum bicolor</i> ≥ 0.20 to < 3 m tall (DaC)	All	0.093 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (All Sub)	GC	-0.137 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (All Sub)	GC & LUS	-0.423 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (All Sub)	LUS to C	0.171 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (All Sub)	HUS to C	0.210 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (All Sub)	All	-0.118 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (Soil)	GC	0.107 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (Soil)	All FPC	-0.114 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (CWD)	LUS to C	-0.295 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (CWD)	All	-0.431 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (FC)	LUS to C	0.442 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (FC)	All	0.037 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (DaC)	LUS to C	0.134 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (DaC)	HUS to C	0.154 ns
<i>Tasmannia lanceolata</i> < 0.20 m tall (DaC)	All	0.002 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (All Sub)	GC	-0.557 *
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (All Sub)	GC & LUS	-0.544 *
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (All Sub)	LUS to C	-0.215 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (All Sub)	HUS to C	-0.238 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (All Sub)	All	-0.485 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (Soil)	GC	-0.175 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (Soil)	All	-0.448 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (CWD)	LUS to C	-0.029 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (CWD)	All	-0.067 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (FC)	LUS to C	0.153 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (FC)	All	-0.203 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (DaC)	LUS to C	-0.168 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (DaC)	HUS to C	-0.226 ns
<i>Tasmannia lanceolata</i> ≥ 0.20 to < 3 m tall (DaC)	All	-0.448 ns
<i>Olearia argophylla</i> < 0.20 m tall (All Sub)	GC	0.126 ns
<i>Olearia argophylla</i> < 0.20 m tall (All Sub)	GC & LUS	0.080 ns
<i>Olearia argophylla</i> < 0.20 m tall (All Sub)	LUS to C	-0.497 *
<i>Olearia argophylla</i> < 0.20 m tall (All Sub)	HUS to C	-0.523 *
<i>Olearia argophylla</i> < 0.20 m tall (All Sub)	All	-0.388 ns
<i>Olearia argophylla</i> < 0.20 m tall (Soil)	GC	0.273 ns

Table continued next page

Appendix Table 6.1 Continued

Frequency	Stratum/s	Correlation Result
<i>Olearia argophylla</i> < 0.20 m tall (Soil)	All	-0.113 ns
<i>Olearia argophylla</i> < 0.20 m tall (CWD)	LUS to C	-0.168 ns
<i>Olearia argophylla</i> < 0.20 m tall (CWD)	All	-0.005 ns
<i>Olearia argophylla</i> < 0.20 m tall (FC)	LUS to C	-0.227 ns
<i>Olearia argophylla</i> < 0.20 m tall (FC)	All	-0.081 ns
<i>Olearia argophylla</i> < 0.20 m tall (DaC)	LUS to C	-0.459 ns
<i>Olearia argophylla</i> < 0.20 m tall (DaC)	HUS to C	-0.410 ns
<i>Olearia argophylla</i> < 0.20 m tall (DaC)	All	-0.321 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (All Sub)	GC	0.308 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (All Sub)	GC & LUS	0.036 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (All Sub)	LUS to C	-0.343 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (All Sub)	HUS to C	-0.204 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (All Sub)	All	0.252 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (Soil)	GC	0.453 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (Soil)	All	0.338 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (CWD)	LUS to C	NA
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (CWD)	All	NA
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (FC)	LUS to C	NA
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (FC)	All	NA
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (DaC)	LUS to C	-0.255 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (DaC)	HUS to C	-0.211 ns
<i>Olearia argophylla</i> ≥ 0.20 to < 3 m tall (DaC)	All	0.055 ns